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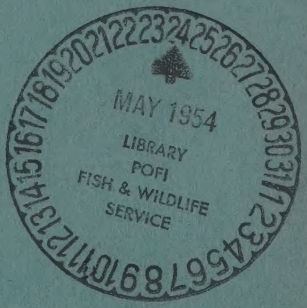

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BULLETIN OF MARINE SCIENCE
OF THE GULF AND CARIBBEAN

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BULLETIN OF MARINE SCIENCE
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AN IMPROVED CAMERA FOR ONE-DIMENSIONAL REDUCTION OF FATHOGRAMS[1]

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ABSTRACT

A camera is described which photographs elongate traces, such as fathograms, producing in one dimension a reduction which is four times that in the other dimension. This ratio is variable. This is an improvement on an earlier model in that it allows longer records to be photographed without reloading the camera and also in being adaptable to varying widths of records.

Automatic recorders frequently produce records in long, narrow strips, whose dimensions are unsuitable for study or reproduction. In such cases it may be desirable to contract the records horizontally, leaving the vertical dimensions unchanged. In an earlier publication (Moore, 1949), a camera was described which achieved this photographically. That model, however, suffered from certain disadvantages. In the first place, the record was transferred to cut film or plates and these had to be changed after a comparatively short length of the original record had been scanned. In the second place, the scanning device was less smooth in action than could have been desired, tending to produce strips of varying exposure across the plate.

The present model was originally built at Woods Hole Oceanographic Institution and used solely for fathograms from an N.M.C. 1. type echo-sounder. It was later modified at Miami to allow other types of record to be handled. The author is indebted to the staffs of both laboratories for advice and assistance, and to Mr. D. L. O'Berry of the Marine Laboratory for the photographs used in this report.

1 Contribution No. 93 from the Marine Laboratory, University of Miami.

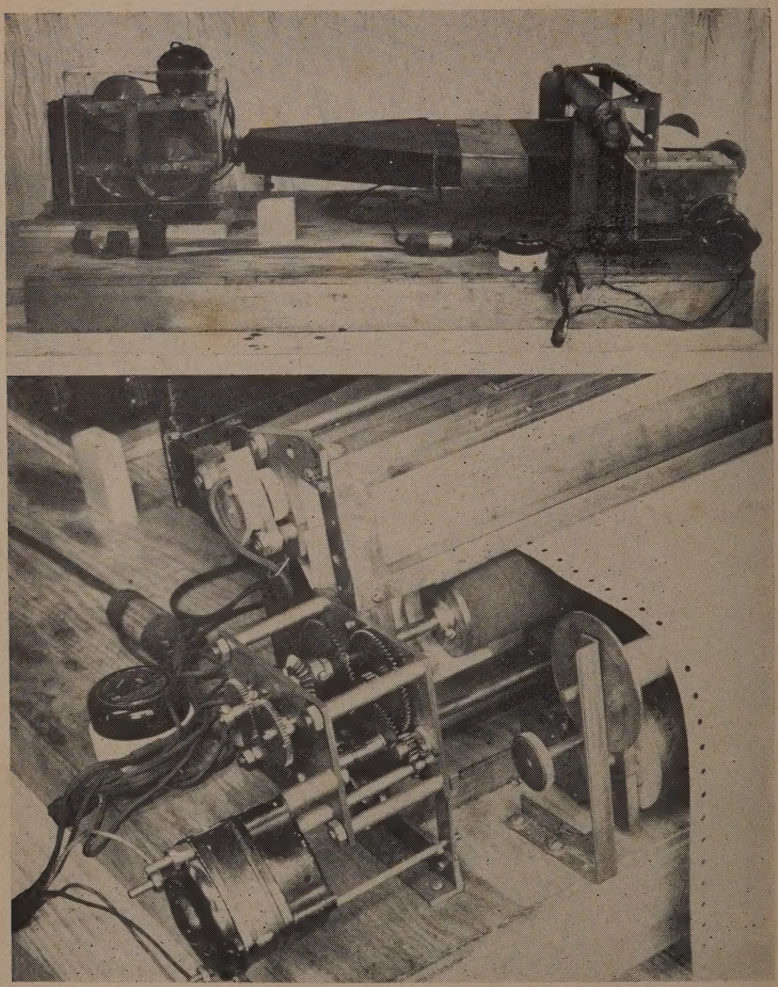

FIGURE 1. Above, front view, with scanning unit on right. Below, detail of driving mechanism for scanning unit, and end of rubber roller. The record shown is narrower than the full capacity of the roller.

Scanning Unit (Figure 1). Fathogram rolls, up to ten inches wide, are carried on their own spools within the end frame. With spools of smaller sizes, stops are attached to keep the rolls centered. From the spool, the paper passes round a rubber-covered roller, against which it is pressed by two small, free-turning rollers, also rubber-covered. The spacing of the latter can be varied to suit the size of record in use. They are so mounted that they can be moved aside to facilitate the insertion of paper. Two brass guide strips overlap the edges of the paper and keep this pressed close to the roller as it passes the scanning slit.

The rubber roller is driven, through a series of reduction gears, by a 1/50 H.P., 60 r.p.m. motor. The gears normally used are designed to give a 4 : 1 horizontal reduction in the records, but a gear shift is provided to give 1 : 1 reproduction when required, and other ratios could readily be incorporated. A counter, coupled to the gear train, is calibrated to show the amount of record run over the roller.

The record is scanned through a slit, 1 mm. in diameter, between two brass strips. These strips are locked in slots in the supporting frame, and can slide in these slots for adjustments of the slit size. The slit is 10 mm. from the face of the record. In the space between, and just above and below the level of the slit, are the apertures in the reflectors round the two lamps. These illuminate the part of the record being scanned. The two lamps are 60 watt tubular filament type, with frosted surfaces, and are housed in polished aluminum reflectors.

Connector Unit (Figures 1 and 2). The scanning unit is connected with the camera unit by a light-tight metal housing. This is built with a telescoping joint to allow the camera distance to be varied. The inside is painted black, and two pairs of transverse baffles are provided to reduce internal reflection. This could probably be achieved more readily by coating the inside with black flock.

Camera Unit (Figure 2). This consists of a 35 mm. movie camera from which practically all the internal mechanism has been removed. The only parts retained are the sprocket round which the film travels, and the gates which hold the film against the sprocket. There is no shutter, and no spools are used, the film lying free inside the camera case. The only difficult part in the construction of the camera lies in the provision of extremely uniform movement of the film. Any irregu-

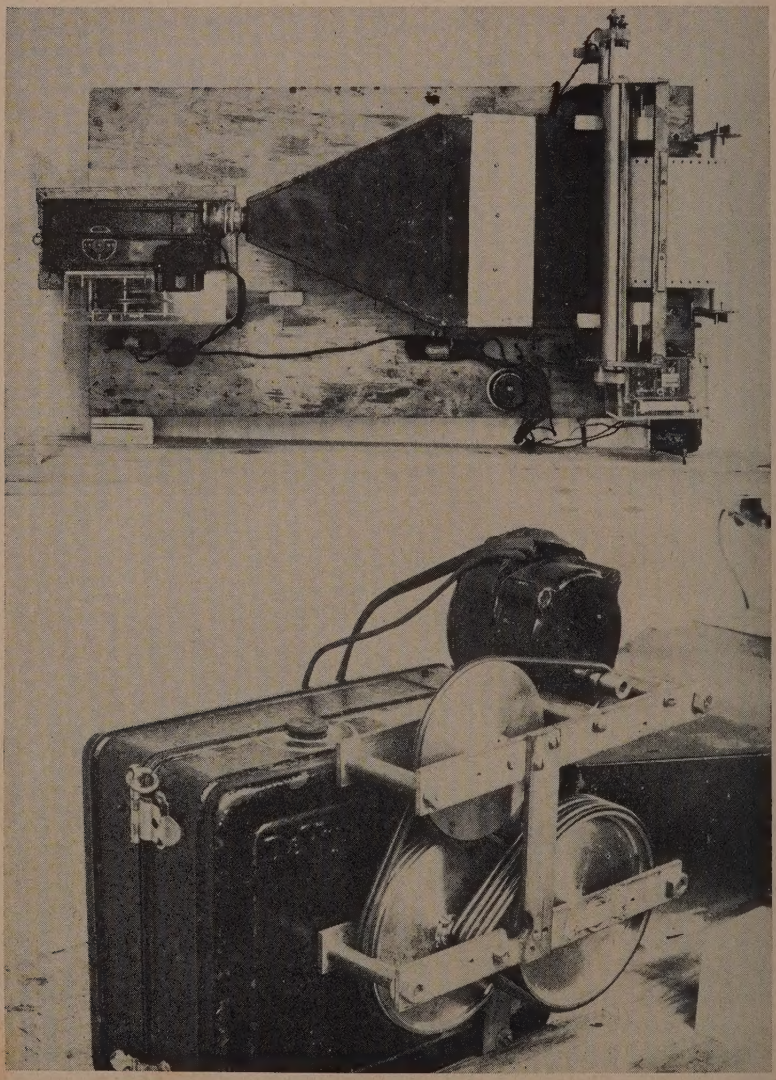

FIGURE 2. Above, top view, with camera unit on left, x 1/10. Below, detail of driving mechanism for camera unit.

larity results in transverse bands of varying exposure, and a corresponding fluctuation in the contraction ratio. After trying several types of gear drive which proved unsatisfactory, a belt drive was incorporated, and this proved sufficiently smooth in action. Power is derived from a second motor, similar to that which drives the record. The three-stage reduction gear uses "O-rings" as belts, one in the first stage, two in parallel in the second, and five in the third. The original bearings of the sprocket axle have been replaced with ball races.

Operation. With Eastman's plus-X film, the best exposure is obtained at an aperture of f.22, and with Eastman's "Microfile" film, of f.8. The latter gives finer grain, but with the present lens, the small aperture is preferable. The paper record runs through the machine at a rate of 44 cm. per minute. As pointed out in the description of the earlier model, the one-dimensional reduction obtained has the added advantage of producing a corresponding reduction in the degree of curvature of the vertical ordinates of those fathograms which are traced by a revolving stylus arm. On the other hand, any lettering on the original record is also distorted, usually to a point at which it is unreadable, and any legend must be written in horizontally elongate symbols.

REFERENCE

MOORE, H. B.
1949. A camera for producing one-dimensional reduction in narrow records. J. Mar. Res., *8* (1): 21-23.

QUANTITATIVE MEASUREMENT OF THE EFFECT ON OYSTERS OF DISEASE CAUSED BY *DERMOCYSTIDIUM MARINUM*[1]

SAMMY RAY[2], J. G. MACKIN[3], AND JAMES L. BOSWELL[4]

ABSTRACT

Measurement of effect of the *Dermocystidium* mycosis in terms of weight of oyster meats has been accomplished by analysis of measurements of meat weights and shell capacity of 508 oysters over a period extending from April 1952, to August 1952. The 508 oysters included 198 heavily infected with *D. marinum*, 83 moderately infected, and 227 either lightly infected or negative. Weights of meats of heavily infected oysters and moderately infected oysters are compared, per unit of shell capacity, with the negative and lightly infected group. The data show that the average mean of meat weights of heavily infected oysters was about 33 per cent less than that of the controls and that the moderately infected oysters were intermediate in loss of weight. Mathematical analyses of the data support the conclusion that disease plays a major role in reduction of meat weights.

Analysis of the data also shows that reduction of weights is not only a matter of disease but of season, summer losses accruing from disease being significantly greater than those of early spring months.

Experimental studies which eliminate factors of nutrition point to lysis of tissues as one of the major processes resulting in loss of weight. In these studies reduction of bits of excised gill tissues which were heavily infected with the fungus is compared with that of normal excised tissues when bacterial and other contaminants are excluded.

Statistical methods and procedures are fully described.

INTRODUCTION

It has been pointed out (Mackin, 1951) that an important effect of parasitization of oysters by *D. marinum* is lysis of host tissues. This lytic action of the fungus is obvious when comparisons are made of

[1]Contribution No. 23 from the Department of Oceanography of the Agricultural and Mechanical College of Texas. This paper was presented November 20, 1952, at the Fifth Annual Session of the Gulf and Caribbean Fisheries Institute, Miami Beach, Florida.
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[4]Texas A. & M. Research Foundation, Grand Isle, Louisiana.
*See text for explanation of symbols and period groups.
* Periods 4 and 5 combined.
* 95 per cent confidence limits
*95 per cent confidence limits
**Hoel, P. G., Introduction to Mathematical Statistics, Wiley, 1947, p. 89.

tissue sections of normal uninfected oysters and those with massive infections. However, measurement of the weight of tissue destroyed by the parasite as the sum total of the effect of the disease has not been accomplished previously. It has been the aim of the present study to determine the extent of destruction of host tissue as a result of the mycosis. It was expected that the data thus derived would serve as a basis for estimation of financial loss to the oyster industry occasioned by the presence of the disease in Louisiana oyster-producing waters.

No attempt has been made to assess the manner of solution of tissue, or the enzymes involved. However, as a separate study, the senior author is now carrying on such studies, and the data will be presented by him at a later date.

R. O. Reid of the Department of Oceanography, Texas A.&M. College, has analyzed the quantitative data presented in this paper and his conclusions regarding significance of the data are included in an addendum. The authors take this opportunity to acknowledge the collaboration of Mr. Reid. Mr. Fred Cauthron of the Grand Isle Laboratory has made most of the photographs.

Statistical Analysis of the Relation of Wet Weight of Meats to the Shell Capacity

Methods. In this study it has been assumed (1) that there is a normal relation betweeen the cubic capacity of the oyster shell and the weight of the oyster meat contained therein, (2) that this relation could be established by measurement of the wet weight of the meat and of the capacity of the shell of a statistically representative number of normal uninfected oysters, and (3) that diseased oysters would not conform to the normal relation thus established but would show a lesser mean weight for any given shell capacity. This last assumption was based on the observed fact that most of the heavily diseased oysters were shrunken in appearance, when the meats were compared with the shell size. Also, it seemed reasonable that even a severe disease would not produce marked change in shell capacity. Shell capacity therefore could be depended upon to remain relatively static during severe disease while the meats, actually attacked and occupied by the fungus, would be reduced in weight, thereby resulting

in a change from the normal relationship of shell capacity to weight of meats.

So far as the entire oyster meat is concerned, the time of maximum intensity of infection is marked by gaping. Concentrations of parasites at this time are usually heavy, although a few oysters gape with only moderate infections. As a means of obtaining data on weights and shell capacities of heavily infected oysters, therefore, gapers were collected from a population of approximately two-year-old oysters. This population was kept in Sea Rac trays at the Grand Isle Laboratory of the Texas A.&M. Research Foundation. Trays were examined for gapers daily or twice daily in the period from April 4, 1952, to August 30, 1952. Not all gapers recovered were in acceptable condition, since only those free from bacteria or other saprophytes were used in the study, and only those in which the tissues were still alive as shown by ciliary action of gills, by heart beat, or by sensitivity of the mantle margin. Those few gapers found to have died from causes other than the *Dermocystidium* mycosis were discarded.

During the period of the study, 176 gapers were found to have heavy infections and were in suitable condition for use. Additionally, checks of non-gapers revealed 22 oysters heavily infected, which were added to the heavy group derived from gapers, making a total of 198 heavily infected oysters analyzed for shell capacity and wet weight of the meats.

At the beginning of the study a small group (25) of non-gapers was analyzed for presence and intensity of disease, and the shell volume and wet weight of the meats were measured. Some of these were normal and uninfected while others showed light, moderate, or occasionally heavy disease. Subsequently, when a gaper was found in a tray and analyzed for disease, volume of shell, and wet weight, a non-gaper was random-selected for a control, and subjected to the same analyses. These analyses were made, a few each day or week, throughout the period of the study. Data bearing on comparative weights of oysters of different disease classes were thus cumulative. Toward the termination of the study, incidence and intensity of infection had so increased that insufficient numbers of control (uninfected) oysters were being taken, so that it was necessary to double the number of live oysters random-selected for each gaper. Additionally, a group of 14 non-gapers was taken for analysis toward the end

of August when data-taking ended. The total number of non-gapers analyzed was 332.

The Ray method (Ray, 1952) was used in all diagnoses of disease and estimations of intensity of disease. On the basis of intensity of infection, the non-gaper controls were divided into four groups, those negative for *Dermocystidium,* those with light infections, those with moderate infections, and those determined as having heavy infections. As stated above, the last group was joined with the heavily infected gapers in the final tabulation of data.

By the cumulative method described, weight and shell volume data were acquired for 227 oysters negative or with light disease, 83 oysters with moderate disease, and 198 with heavy concentrations of the parasite. These three classes were compared as to meat weight, using the following statistical methods:

1. Comparison of the distribution of points on scatter diagrams of the different disease classes, in which the shell capacity of each oyster was plotted against the wet weight of the meat.

2. Comparison of the slopes of calculated regression curves derived from the regression of meat weights on the shell volumes.

3. Comparison of arithmetic means of weights of the oysters of the different disease classes, when adjusted to unit volume of shell capacity. This method was applied to the entire period of the study, which was then divided into successive time periods in order to provide a means of measuring the effect of seasonal changes.

Measurement of volume of shell was accomplished by the following steps. First each oyster was thoroughly cleaned of all loose adhering mud or debris. Then the volume of the shell was measured by the water displacement method, using a specially constructed vessel with an inclined spout and inserted fine wire to break the surface tension meniscus. If the oyster was a gaper, the valves were clamped shut by means of a small screw clamp. If such oysters could not be sealed a paraffin cast of the shell cavity was made and the volume of the cast was measured by displacement. After removal of the meat from the shell, the volume of the separated shells was measured and this volume was subtracted from the volume of the closed shell, the difference being the volume of the internal cavity.

Using a small laboratory balance, meats of the oysters were weighed, after a standard blotting period designed to remove excess external moisture. Each oyster meat was blotted on a standard toweling paper

for five minutes; it was then turned over and blotted for another five minutes. After weighing, a portion of the posterior gut was removed and cultured for two or three days in thioglycollate medium (see Ray, 1952). Streptomycin and penicillin were added to prevent the growth of bacteria. At the end of the culture period, the tissues were examined and the intensity of infection with *Dermocystidium* was recorded.

A mantle portion was removed from each oyster and fixed in Zenker's fluid. This was a precautionary measure to make possible the recognition of such parasites as *Bucephalus,* which might confuse the data. Gapers found to be parasitized by organisms other than *Dermocystidium* were eliminated from the calculations.

It is necessary at this point to redefine the three intensities of infection. The original definition (Mackin, 1951) was designed for diagnosis from stained sections. The Ray technique, however, combines radically increased size of the parasites with iodine staining, which latter imparts a blue color to the thickened cell walls. A considerable block of tissue can be studied for the parasites. Using this method, heavy infections are those in which the major part of the tissue, treated with iodine, appears macroscopically to be a dull green-blue to black color. The color is due to the enormous numbers of parasites since the oyster tissue does not stain blue, but remains yellow or yellow-orange. It is not necessary to examine such tissues under the microscope to diagnose heavy infection, but microscopic examinations were made throughout the study.

A moderate infection is one in which cells of the parasite are numerous in the tissues, but in which local areas, when observed microscopically, show definite concentrations, while others are relatively free from parasites. Such moderate infections are usually insufficient in concentration to be observed macroscopically although the tissues may be slightly tinged with blue color.

A light infection is one in which the parasites in the test tissue are few in number. In most cases microscopic search is necessary to establish their presence. Light infections vary from one to several cells up to a light scattering of isolated cells or small clumps of cells, but do not show proliferating masses of cells.

It is to be noted that a heavy infection is sharply separable from a light infection, while the moderate infection is largely a matter of a personal concept, grading as it does into light infections on the one hand and into heavy infections on the other. The beginner in using

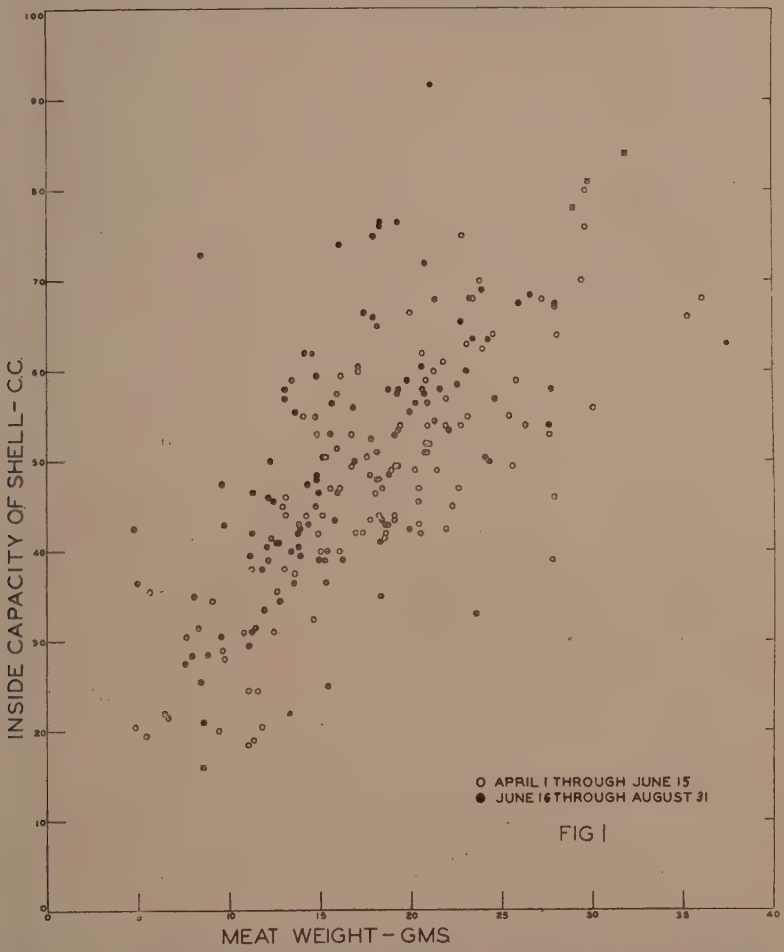

FIGURE 1. Scatter diagram showing the relation of wet weight of meats to shell capacity in oysters lightly infected or negative for *Dermocystidium* disease. The data are based on measurements of 227 oysters.

the Ray method is quite apt to overestimate the intensity of infection. It is possible also that in a small percentage of cases, negative diagnoses have been made on the basis of the culture of the posterior gut, when

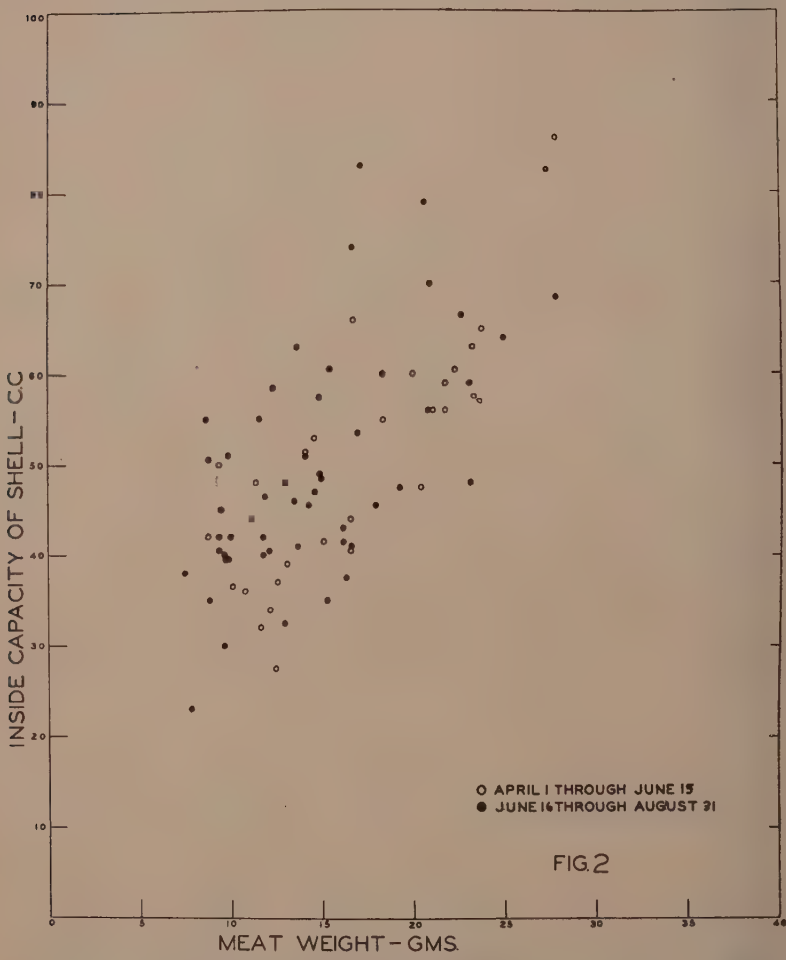

FIGURE 2. Scatter diagram showing the relation of wet weight of meats to shell capacity in oysters with moderately intense infections of *Dermocystidium*. The data are based on measurements of 83 oysters.

light infections may have occurred in other parts of the body. Checks have shown, however, that such cases are few in number; they could not affect the validity of conclusions in the present study, since for

purposes of analysis, the lightly infected and negative oysters are grouped in a unit.

Results. The results of measurements of wet weight vs. shell capacity are shown in Figs. 1 to 5. Fig. 1 is a scatter diagram for the combined light and negative oyster class, Fig. 2, for the moderate infection class, and Fig. 3, for the heavy infection class. Examination of the scatter of points of Fig. 1 indicates that the relation of wet weight of the meat to shell capacity is linear. Study of the data showed that from a statistical standpoint, loss of weight in those oysters lightly infected was not significant. For this reason this group was united with that of the uninfected oysters as a means of producing greater statistical reliability. The wide scatter of the points is partly produced by the time element. The studies necessarily were extended over a period which began with oysters near maximum in condition in April, and which included the spawning period and the following summer. The period from April to August is one of naturally declining relative and actual weight in Louisiana oysters.

A comparison of the three scatter diagrams shows that as infection intensity increased, the points moved progressively toward the lighter weights, *i.e.*, toward lesser weights of meat per unit of shell volume. It will be noted that two kinds of points are plotted in the three diagrams, open circles and solid circles. Open circles represent oysters analyzed prior to June 15, and the solid circles those analyzed after that date. There is a tendency of the open circles to lie to the right reflecting a generally better condition of the oysters in early spring over those in summer. This difference is not great in normal oysters, but is more pronounced in moderately infected oysters and quite marked in those heavily infected.

Calculated regression curves showing the relation of wet weight to shell capacity are shown in Fig. 4, which compares the slope of the calculated curves for all three classes of oysters. To avoid the large number of points included on the scatter diagrams, the points were averaged for each ten cubic centimeter interval of shell capacity except at the extremities of the curves where a somewhat wider interval is used. The weighting factor for each point is given in Fig. 4. The slope for each curve is also given. For normal oysters, the slope was calculated as 0.354. It decreased with increasing intensity of disease to 0.242 in heavily infected oysters. Significance of the data is discussed in a later section.

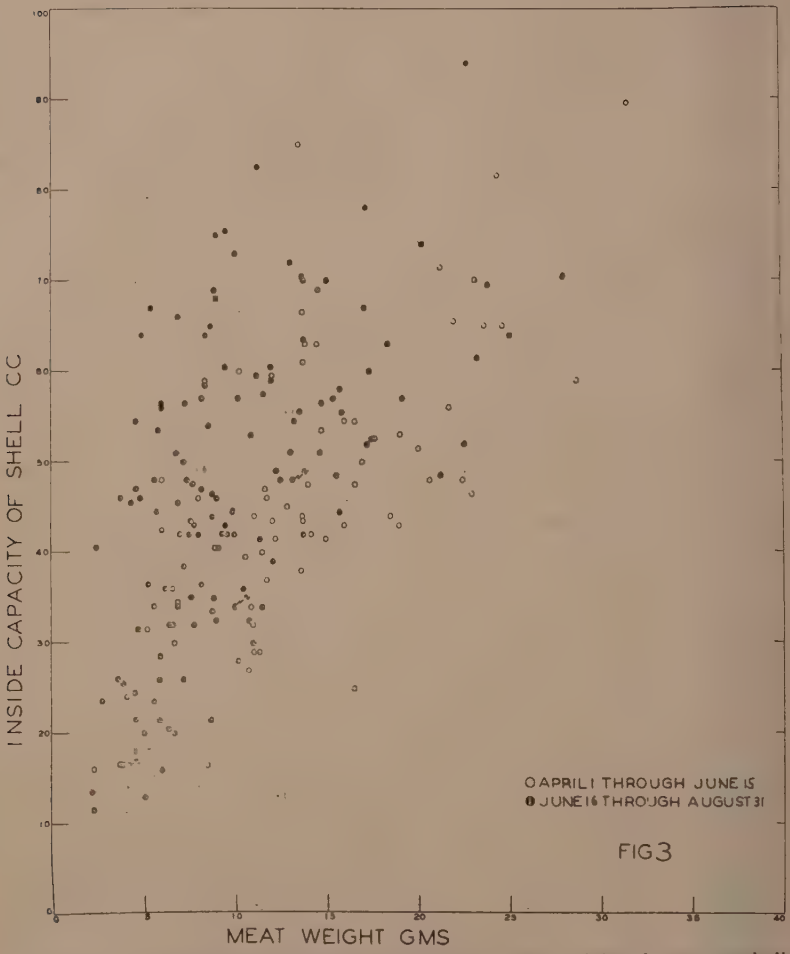

FIGURE 3. Scatter diagram showing the relation of wet weight of meats to shell capacity in oysters heavily infected by *Dermocystidium*. The data are based on measurements of 198 oysters.

From the statistical point of view, weights of lightly infected oysters were not significantly lower than those of negative oysters. But biologically speaking, light infections must have an effect if it be demon-

strated that moderate and heavy infections have a significant effect. In this case, there can be no question but that moderate and heavy infections produce significant losses of weight. Since that is true, it is also necessarily true that the effect must begin somewhere in the early stages of disease. Actual comparisons of weight means for negative and lightly infected oysters showed that the loss amounted to between 8 and 9 per cent per unit of shell capacity. Thus the union of lightly infected and negative groups into one class is a measure of conservatism in calculation.

It was recognized that since heavily infected oysters must be collected over a considerable period of time, it was necessary to have controls distributed over the same period. That period (April to August) was one in which (1) spawning on a heavy scale regularly took place, and (2) condition of the oyster meats normally deteriorated in warm weather. Therefore, the extent of the normal deterioration was measured and compared with that of diseased oysters, and the amount of loss of weight of oysters due to disease in different periods was computed. For these calculations, the wet weights of each of the three classes of oysters were averaged for successive sub-periods of the total period of data-taking. These average wet weights were reduced to weights per unit of shell capacity and plotted against time on coordinate paper. Fig. 5 presents a summary of the data so derived. The curve for the negative-light class shows clearly the relative loss of weight during the heavy spawning period, then a period of partial recovery, followed by another loss. The latter is unexplained unless it represents a second spawning period. It is also possible that it is a result of a combination of gonadal exhaustion and weakening by shell pests (*Polydora* especially), which heavily invaded the shells of the experimental population in the latter part of the summer.

A comparison of the mean weights per unit capacity of normal oysters with those of moderately and heavily infected oysters shows the same progressive loss of weight due to disease. A study of Fig. 5 shows that loss to the mycosis is much more significant than loss to spawning or other cause, for oysters heavily infected average less weight per unit shell capacity prior to the spawning period, than do the normal oysters at the end of the heavy spawning period. Heavily diseased oysters also show a more drastic drop in weight during the late summer than do the normal oysters. As would be expected, moderately infected oysters stand in an intermediate position between the normal

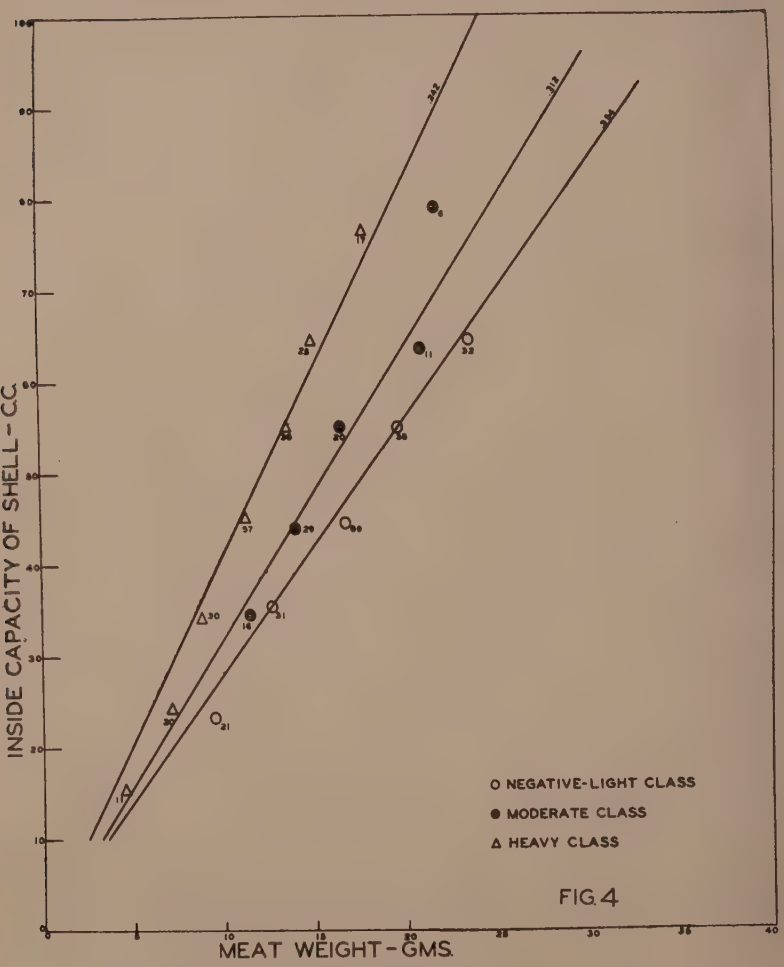

FIGURE 4. Regression curves showing slopes for three classes of oysters for which scatter diagrams are plotted in Figs. 1-3. Points are for wet-weight means of intervals of 10 cubic centimeters of shell capacity, excepting the extremes where intervals are somewhat greater.

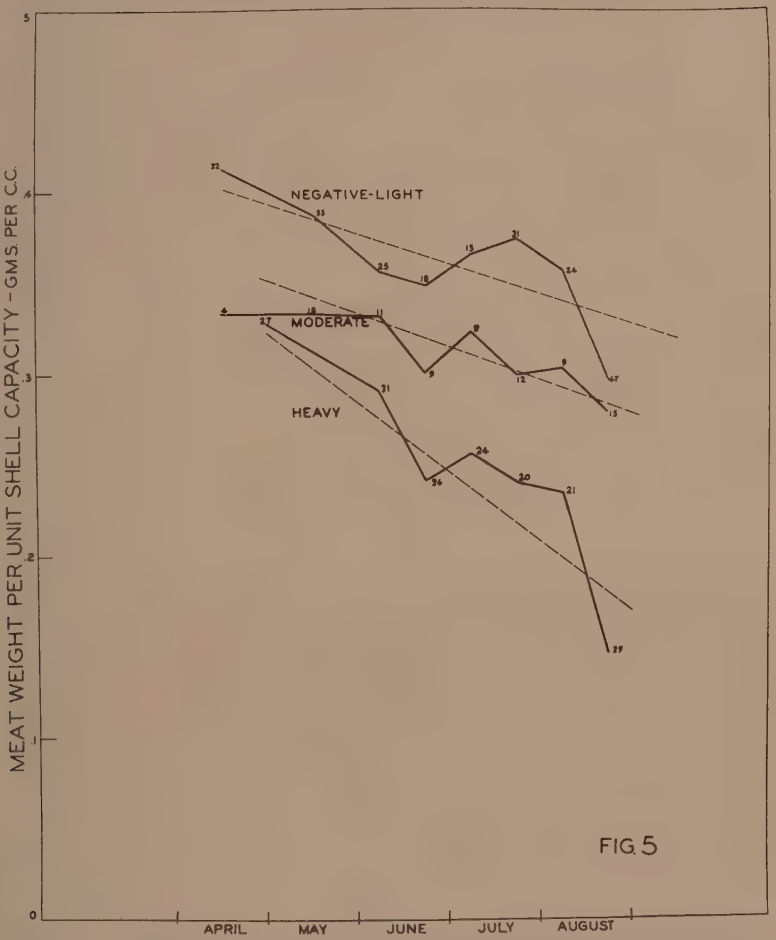

FIGURE 5. Means of wet weights of meats per unit of shell capacity for three disease classes of oysters plotted against time. Straight lines are calculated slopes. Numbers beside the points give the number of observations for each point. The sag in the curve for the negative-light class reflects the weight losses during spawning.

ones and those heavily infected. In the April-May period, average loss of weight due to disease in heavily infected oysters amounted to

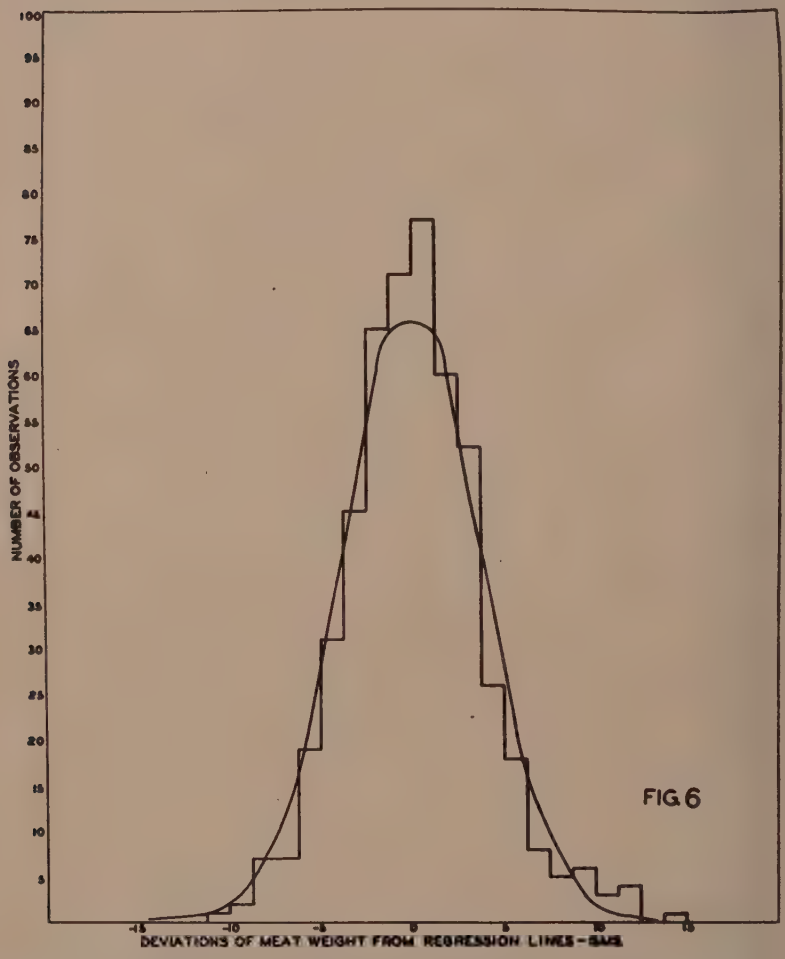

FIGURE 6. Histogram of the distribution of deviations of meat weights from the regression lines of Fig 4. The solid line curve represents the normal distribution of the deviations as calculated, with zero mean and standard deviation equal to that computed for the observed histogram (S = 3.7 gms.)

slightly less than 20 per cent; in the latter part of August, heavily infected oysters averaged only about half the weight of normal oysters. Thus the effect of the high temperature of summer is reflected not only in increased mortality from disease, but also in radically decreased meat weights. Moderately infected oysters averaged about 12 per cent loss of weight in the early spring and about 15 per cent, during the latter two weeks of August.

Experimental Disintegration of Isolated Tissues of the Oyster by Dermocystidium

Methods. In the course of culturing studies on *Dermocystidium marinum,* it had been observed that tissues removed from heavily infected oysters disintegrated rapidly even when protected from bacterial attack. Recognizing that this fact offered a method for studying the effect of the parasites, a series of studies was set up as a means of comparing normal uninfected tissues with those heavily infected. The steps were as follows.

Small pieces of gill tissue were removed from gapers and placed in sterile Carrel tissue culture flasks containing a small amount of sterile sea water. Streptomycin and penicillin were added to the water to insure that no bacterial invasion of the tissues occurred. All gill tissues used were alive as shown by examination of the cilia. Prior to excisement of the bits of tissue, each oyster was (1) washed thoroughly with sterile sea water, (2) washed with a solution of sodium merthiolate (1 to 10,000) for about 10 minutes, (3) washed again in sterile sea water, (4) allowed to remain in sterile sea water fortified with 1000 units each of streptomycin and penicillin for several hours. Portions of gill tissue were then placed in Carrel flasks in sea water fortified with antibiotics. The neck of each flask was plugged with sterile cotton. The plug was held in place by a small rubber sleeve. In some cases, a dilute lysol solution was substituted for the sodium merthiolate. The pretreatment cannot be a sterile one, so far as yeasts, molds and protozoa are concerned, and was designed to relieve the oyster of adhering spores and cysts. Failures to prevent contamination were frequent, much more frequent than were successes, and most of the experiments were discarded because of the appearance of contaminating molds, yeasts, or ciliate protozoans. The latter were particularly troublesome. Yeasts are so slow in development in such a medium

FIGURE 7. (left) Photograph of a unit study of lysis of excised gill tissues, made July 17, 1952, when the study was initiated. Carrel flasks in vertical rows marked "E" contain gill tissues heavily infected with *Dermocystidium;* those marked "C" are uninfected controls.

FIGURE 8. (right) Photograph of the Carrel flask lysis study shown in Fig. 7, taken on July 23, 1952. The cloudiness of the controls was caused by diapedesis of leucocytes.

that only occasional contamination resulted therefrom. Aquatic molds were nearly as frequent contaminants as were the ciliate protozoans. Molds also were slow to appear and in most cases did not show up until disintegration of the tissues was far along. Some of the studies were successful in eliminating all contaminants, leaving only *Dermocystidium* cells in the tissues.

Controls were set up in exactly the same manner as were the experimental studies. It was necessary to assume that a control oyster was free of infection and to proceed on that assumption until diagnosis was completed. In case a live oyster set up as a control was later found to be infected, it was not necessary to eliminate it as a control if the intensity of infection was very low. However, such partial controls were not considered to be desirable and were not used in the comparisons.

Six control flasks and six experimental flasks were set up in each unit study. Photographs were made at the beginning of each study and again at an intermediate stage and at the end of each study. These recorded the progress of disintegration of the tissues. Contents of all flasks were examined microscopically at the end of each study to determine whether or not contaminating organisms were present. *Results.* Results of the studies of lysis of excised tissues are illustrated in Figs. 7, 8 and 9. Fig. 7 is a photograph taken at the time tissues were placed in Carrel flasks on July 17, 1952, Fig. 8 was taken a week later, and Fig. 9, on July 31, 1952, at which time the experiment was brought to a close.

The results are obvious from the photographs. Tissue parasitized by *Dermocystidium marinum* was completely disintegrated in all six experimental flasks. A few active ciliated cells from the gill epithelium were found in the experimental flasks at the end of the study, but, aside from these, little material identifiable as originally part of the gill tissue remained. The granular debris left consisted almost entirely of masses of *Dermocystidium* cells. A photomicrograph of these is shown in Fig. 10. The spheres are cells of *Dermocystidium*. One experimental Carrel flask culture (bottom, first row in Fig. 9) was contaminated by a mold; all others were free from contamination.

Controls were free of contamination excepting in Carrel flask number two of the last row, which was occupied by a mold. All tissues were still intact and with ciliary movement, even that piece attacked by the mold. It is to be noted in Fig. 8 that control flasks were cloudy in appearance. This was due to diapedesis of masses of

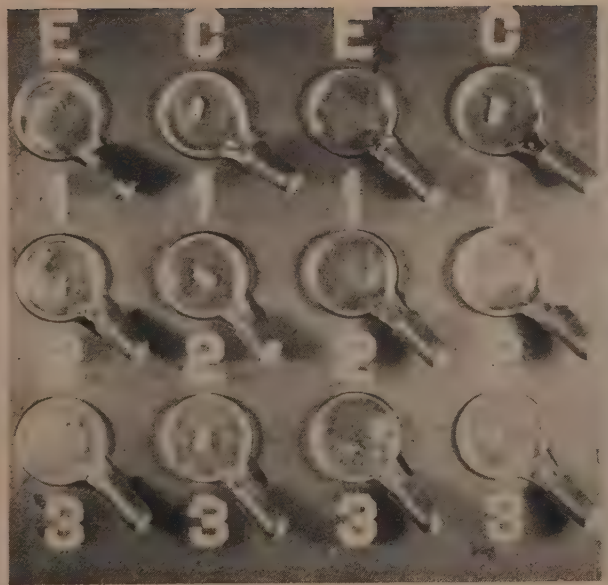

FIGURE 9. (lett) Photograph of the Carrel flask lysis study shown in Figs. 7 and 8, taken on July 31, 1952, when the study was concluded. Note the nearly complete destruction of parasitized tissue. Shrinkage of controls was caused by diapedesis of leucocytes and by autolysis. Control tissues were still alive except the piece in the second flask of last row, which was attacked by a mold. The third flask in the first row of experimental tissues was likewise contaminated by a mold.

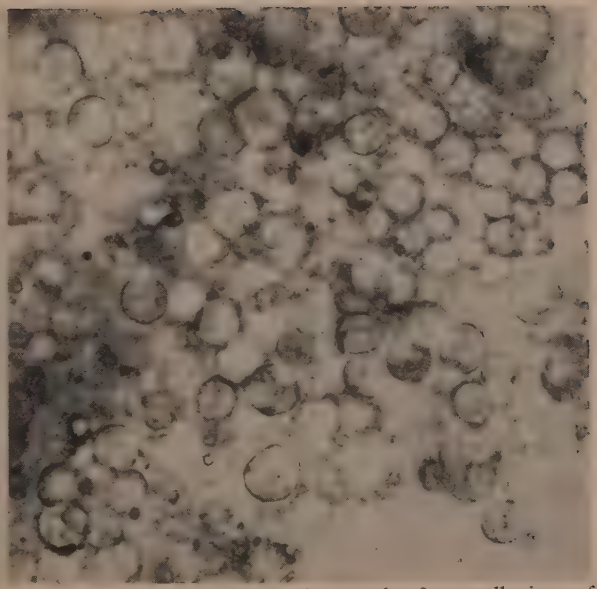

FIGURE 10. (right) Photomicrograph of a small piece of debris taken from one of the experimental Carrel flasks (number one of the left hand row). The original tissue is now replaced almost completely by *Dermocystidium* cells, the minute spheres making up most of the fragment, unstained.

leucocytes which moved out of the tissues into the dish. Few of these were in the experimental flasks, since most leucocytes are occupied by parasites in heavily infected oysters and are destroyed as fast as they are formed. Shrinkage of the control tissues was due to combined autolysis and loss of leucocytes by diapedesis. Just before the photograph, Fig. 9, was taken, the leucocytes were removed by pipette, so that the flasks are not clouded in the last photograph. After this photograph was taken, the cultures were examined and discarded.

After an oyster has gaped under natural conditions in the field, disintegration of the tissues is largely accomplished by saprophytic bacteria, water molds and ciliates. The role of *Dermocystidium* is probably minor in that post-gaping period. The experiment just described is therefore useful only in the interpretation of the action of *Dermocystidium* cells on the host. A close study of the progress of the decomposition of the tissue suggests that the principal action of the parasites is on the intercellular binding materials, closely paralleling that of certain animal parasites. The nature of the substance or substances utilized by *Dermocystidium* in breaking down tissue is under investigation by the senior author.

Discussion. The data presented show that one effect of parasitization of oysters by *Dermocystidium* is marked loss of weight. The statistical data do not indicate the manner in which the parasite brings about such an effect, whether it is largely lytic or whether it stems from some other source, such as induced starvation. Histological studies on heavily infected oysters show that they do not feed in late stages of infection, but do while lightly or moderately diseased. However, ingestion of food does not prove that it is either digested or assimilated. It is quite possible that even light disease may seriously interfere with these functions.

The studies on disintegration of isolated gill tissues indicate strongly that the major effect of disease is lysis. In these studies, no feeding of the oyster was involved. The rapid dissolution of parasitized tissues (compared with the slow autolysis in control tissues) can only be charged to production of a lytic enzyme.

Irrespective of the exact manner in which it is accomplished, the studies here presented show conclusively that the *Dermocystidium* mycosis effects drastic loss of weight in infected oysters. Moderate infections produce 12 to 15 per cent loss; those oysters in terminal stages of disease have lost from 20 per cent (in cool months) to 50

per cent (in summer) of the total meat weight. The average loss is about 33 per cent. In terms of economic loss to the oyster industry, it is roughly estimated that in Louisiana the loss amounts to about $250,000 annually. The estimate is based on (1) incidences of *Dermocystidium* infection, in the marketing period of early spring, at seven stations in the area west of the Mississippi, (2) total oyster production in the ten year period of 1940 to 1950 in pounds (Southern Fisherman Yearbook for 1952), and (3) a value of $0.35 per pound. This loss is largely borne by packers. The very much greater loss to oyster farmers by mortality on the beds and aboard boat is not here considered.

The data show also that a major part of the deterioration in condition of Louisiana oysters in summer months, and especially in late summer, is due to mycotic disease. The extremely high incidence of the disease (roughly 50 to 95 per cent) in waters with moderate to high salinity establishes *Dermocystidium* disease as the most important factor operative in the loss of meat weight in such waters.

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ADDENDUM: STATISTICAL COMPUTATIONS

R. O. REID*

The statistical problem related to the oyster data which has been discussed in the main body of this report is formulated here.

Terminology

It is convenient to introduce the following symbols in this discussion:

y = meat weight of an oyster in grams;

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x = shell capacity, *i.e.*, the inside volume of the closed shell of an oyster, in cubic centimeters;

i = subscript denoting an individual oyster in any sample;

t_j = period group, identifying the interval of time during which samples were taken, j ranging from 1 to 8;

I_k = infection class of an oyster at the time sample was taken, where k = 1, 2, 3, 4 indicates the degree of infection;

n_j = number of individual oysters in a sample taken in the period t_j;

n_{jk} = number of individual oysters, taken in the period t_j, which have an infection of degree k.

The notation y_{ijk} indicates an individual sample value of y, which happens to be in the k infection class, taken in the period t_j. The associated sample value of x for the same individual is x_{ijk}. However y and x will be used interchangeably with the sample value notation, unless otherwise specified. For example $\bar{y}_k$ represents the mean value of the samples of y in the k infection class; there are four such mean values. The average above is taken over all period groups; the average y for a given period group and given infection class is denoted as $\bar{y}_{jk}$. There are eight time groups and hence 32 of these averages.

The identification of the infection classes follows the scheme:

I_1 = negative infection (k = 1)
I_2 = Light infection (k = 2)
I_3 = Moderate infection (k = 3)
I_4 = Heavy infection (k = 4)

In the final analysis the classes I_1 and I_2 are treated as one because their sample differences are not significant.

The time groups chosen are not uniform in length because of the variable density of sampling. The groups are denoted in two ways:

Symbol	*Month Designation*	*Actual Period of Sampling*
t_1	4	April 1 to April 30, 1952
t_2	5	May 1 to May 31, 1952
t_3	6a	June 1 to June 15, 1952
t_4	6b	June 16 to June 30, 1952
t_5	7a	July 1 to July 15, 1952
t_6	7b	July 16 to July 31. 1952
t_7	8a	August 1 to August 15, 1952
t_8	8b	August 16 to August 31, 1952

Statement of the Problem

The problem is essentially to evaluate and test the reliability of the dependence of y on the variables x and t for the different discriminating classes I_k; and to determine whether or not the samples taken in the present experiments indicate a statistically significant difference in the inferred relations

$$y = f_k(x, t)$$

The second part of the statement above asks, in effect: do the present data indicate that disease caused by *Dermocystidium marinum* influences the weight of an oyster?

Hypothesis Regarding the Relationship between Y and X

Statistical procedures do not provide the mathematical form of the relationship to be expected between a set of variables. The expected relation is an independent abstraction postulated directly or inferred from postulates which lead to the form of the expected function by inductive procedures. The statistical methods provide means of verifying or nullifying, on a probability basis, the different hypotheses which are put forth concerning a given set of samples of the variables considered.

The working hypothesis which is presumed here is that ratio of weight to capacity (y/x) is not dependent on x but is a function of t, the function being different for each infection class.

Let $M_k(t)$ represent symbolically the functional form of the ratio y/x for different k; thus

$$y = M_k(t)x. \tag{1}$$

This implies that a plot of y versus x for a given t and given infection class should yield a linear relation which passes through the point $x = y = 0$. The slope of this line is $M_k(t)$ and can be evaluated by the method of linear regression wherein the sum of the squares of the deviations of the values of y from the regression line are minimized. The test of the hypothesis concerns (1) the degree of agreement with the condition that $y = 0$ when $x = 0$, and (2) the significance and magnitude of the correlation achieved.

A further assumption which is made is that the deviations of the values of y from the regression lines are normally distributed. That is, it is expected that variations in y which are in no way associated with changes in x, t, or I are present, and beyond the scope of quantitative explanation in the present test. However it is asserted that these latter variations, regardless of their cause, are random and lead to a normal

dispersion of data about the expected relationships. This assumption allows the use of certain statistical tests for the significance of the important coefficients which are sought. A test of the hypothesis of normality of the dispersion of data which is not associated with changes in x, t, and I, indicates that the assumption is justified (see Fig. 6).

The form of the functions M_k (t), at least for the $k = 1$ and $k = 2$ classes, might be expected to be periodic and of annual or semiannual period. However, because of the length of the time interval covered in the experiments, it is not possible to test this hypothesis, and the mathematical form of the functions M_k (t) is left undefined. However, it is possible to use the sample values of M_k as an estimate of the regression curve of the M_k versus time (see Fig. 5), and indicate the range of error that can be expected in the M_k values determined from the set of data at hand.

Graphical Inspection of Y versus X

As a preliminary test of the hypothesis of proportionality of y and x, the scatter diagrams shown in Figs. 1, 2, and 3 were constructed. The scatter of data obscures the general trend such that this graphical test is not conclusive; however, it does not appear that an assumption of non-linearity would be significantly better than that of straight line relation. An improvement in the graphical procedure can be accomplished by smoothing out the dispersion of points. The simplest procedure is to group the values of y for a given infection class in equal ranges of x and evaluate the means y_k for each range of x. A graphical illustration involving averages of this type is given in Fig. 4, where the interval of x is taken as 10 cc., except at the end intervals. In this plot the values of x corresponding to the y in the various intervals are averaged as well. The graph of mean values indicates that the assumption of linearity of y versus x for a given infection class is probably justified and worth testing by more refined statistical methods. Furthermore the figure demonstrates a systematic discrimination associated with degree of infection, and its significance is therefore also worth testing further.

Regression of Y on X

A summary of the basic statistics obtained from the data on the 508 individual oysters tested is given in Table I. The computations give

the breakdown by time groups for each infection class, and present subtotals and total values of those basic parameters which allow calculation of the required regression slopes, correlation coefficients, and standard deviations.

The standard procedure of linear regression by the least squares technique yields, for the grand total statistics of Table I, an intercept of about 2.0 on the y axis. A test of the confidence limits of the regression slope and of the mean value of $\bar{y}$ indicate that this finite value of the intercept is just barely significant (the 95 per cent confidence limits being approximately $\pm$ 1.4). Despite this, the hypothesis of proportionality of y and x is retained (zero intercept of y at $x = 0$). The logic for this choice is essentially that the simple proportionality is more reasonable on the basis of physical considerations. The principal justification however, is that the standard deviation of the points from the regression lines and hence the correlation coefficients are not altered by any significant amount by assuming that the true intercept is zero.

The slope of the most probable line passing through the point $x = y = 0$ is obtained from the relation:

$$M_{jk} = \frac{\Sigma xy}{\Sigma x^2} \quad ; \tag{2}$$

which is the best estimate of the ratio y/x for a given t and I. The summations indicated above refer to sums taken over all values of i in a given class and period group. The standard deviations of values of y from a regression line of this slope is given by

$$S_e^2 = \frac{1}{n}\left[\Sigma y^2 - \frac{(\Sigma xy)^2}{\Sigma x^2}\right] \quad ; \tag{3}$$

and the correlation coefficient is given by

$$r^2 = 1 - \frac{S_e^2}{S_y^2} \tag{4}$$

where

$$S_y^2 = \frac{1}{n}\Sigma y^2 - \left(\frac{\Sigma y}{n}\right)^2 \tag{5}$$

Table II and Fig. 5 give the slopes M_{jk}, representing sample values of M_k (t) or the ratios y/x. Values for each time group (where significant n exist) of three infection classes (the light and negative classes are combined) are presented. The 95 per cent confidence limits of the slopes determined by equation (2) can be determined from the formula

$$(6) \qquad \Delta M = T_{n-2} \frac{\pm Se}{\sqrt{x^2}} \frac{1}{\sqrt{n-2}} ;$$

where T_{n-2} is the Student's distribution function for n-2 degrees freedom at the 95% level, and $\overline{x^2} = \frac{1}{n} \Sigma x^2$.

For $n > 30$, the value of T can be taken as 2, and the distribution of M is normal. The mean values of ΔM for the three classes investigated in Table II, are given below:

	ΔM
Negative and light	± 0.031
Moderate	± 0.060
Heavy	± 0.031

This would indicate considerable overlapping of the distributions of M for the moderate class with the distributions of M in the two neighboring classes. However the negative-light group and the heavy infective group are definitely significantly different through the range of t.

Table III gives the values of the mean slopes M_k for three infection classes and also indicates the 95% confidence limits. The values of M_k were determined from the subtotals of Σxy and Σx^2 of Table I for the moderate and heavy classes. Because of the bias introduced in group 8b of the light class, by virute of the asymmetry of the scatter of points from the group regression slope M_{jk} for the larger values of x, it was deemed justifiable to adjust these data. The bias was counteracted by "rotating" the scatter of points into line with the estimated class mean slope, by merely multiplying the values of y in the whole group 8b of I_2 by the ratio of the estimated class slope to the group slope. This allowed a more reasonable estimate of the class slope (the alteration being slight).

It will be noted from Table III that there is no overlapping of the confidence limits of the M_k as determined by equation (6). This means that the data do indicate that *the three different infection classes represented possess significantly different values of the ratio of weight to capacity as postulated.*

Correlation Coefficients

Rather than to discuss the individual correlations of the various groups or classes, it is sufficient to set forth the gross correlation coefficients of the entire set of data: (a) considering only y and x; (b) considering y, x, and I; and (c) considering y, x, I and t. These

coefficients are denoted as r_{yx}, r_{yxI}, and r_{xyIt}, respectively. The first of these can be obtained from the grand totals of Table I. The second can be obtained by evaluating the mean S_e for all the infection classes (but ignoring t), the third coefficient can be obtained by evaluating the mean S_e, considering deviations of the y from the associated time group regressions rather than from the class regressions. The values of these coefficients and of the corresponding mean standard deviations are given in Table IV.

The confidence limits of r are determined by considering that $\frac{1}{2} \log_e \frac{1+r}{1-r}$ is normally distributed with standard deviation of $1/\sqrt{n-3}$**. The confidence limits of the S_e are determined by the Chi-square theory.

It will be noted that the confidence limits of both the correlation coefficients and the standard deviations do not overlap. Consequently, each of the three values of r and of S_e are significantly different. What this implies is that it is definitely worthwhile to take into account the variation of each of the variables x, I, t, in establishing the expected variation of y, because the value of the overall multiple correlation coefficient for the complete set of variables is significantly superior.

Normality

In applying the various significance tests by evaluation of confidence limits for the regression slopes, correlation coefficients, and standard deviation, it was assumed that y was a normal deviate from the group regression lines. To test this assumption, the histogram of deviations of y measured from each individual regression line (for all 508 points) was compiled, and is shown in Fig. 6. The standard deviation of this distribution is 3.7 (corresponding to the last value given in Table IV). A true normal curve of this standard deviation is shown in the same figure for comparison. The values of skewness and peakedness of the measured distribution are 0.35 and 3.85, which are reasonably close to the values of 0 and 3.0, respectively, for a normal curve.

Finally it is of interest to note that the standard deviations $(S_e)_k$ computed separately for the three classes investigated (not considering variations of y versus t) are:

**Hoel, P. G., Introduction to Mathematical Statistics, Wiley, 1947, p.89.

	$(S_c)_k$	n_k
Negative-Light	4.5	227
Moderate	4.1	83
Heavy	4.8	198

with the mean value 4.5 as given in Table IV. However, the confidence limits at the 95 per cent level for the mean value are 4.2 and 4.8 ($n = 508$) as determined by the Chi-square test. The confidence limits of the individual class values, $(S_c)_k$, are even greater because of the smaller values of n. Consequently one is justified in considering the mean value of 4.5 for all three classes, so far as the data at hand are concerned. This corresponds to the value of $(S_c)_{xI}$ given in Table IV.

Conclusions of the Statistical Analysis

(1) The oyster meat weights are essentially linearly related to the shell capacity for a given season and given degree of infection.

(2) There is a significant difference between the ratio of meat weight to shell capacity for the three different classes of infection (negative-light, moderate, and heavy).

(3) There is a significant seasonal variation of the meat weight for a given shell capacity, for the negative-light class and the heavy class; the data in the moderate group are insufficient to show any significant variation with season.

(4) The light class of infection was found to be not significantly different from the negative class.

(5) The dispersions of y from the mean regression lines of y on x for each class have standard deviations which are not significantly different, and the deviations possess a distribution which is nearly normal.

(6) The overall multiple correlation coefficient of 0.82 indicates that 67 per cent of the variation of y is associated with variations in x, t, and I, while 33 per cent is due to other causes.

TABLE I

SUMMARY OF BASIC COMPUTATIONS*

Infection Class	Period (1952)	n	Σy	Σx	Σxy	Σx^2	Σy^2
	4*	20	454.7	1,081.5	26,505.80	63,110.25	11,550.31
k = 1	5	17	296.2	715.6	13,356.36	32,878.16	5,551.82
	6a	12	219.5	584.0	11,212.55	30,084.00	4,336.31
	6b	8	128.0	381.0	6,301.50	18,891.50	2,212.90
Negative	7a	8	147.2	420.0	7,871.25	22,930.50	2,772.80
	7b	10	189.5	496.0	9,761.25	25,350.50	3,810.41
	8a	8	144.8	393.0	7,848.60	21,446.00	2,917.92
	8b	8	124.8	362.0	6,272.45	18,009.50	2,202.04
	Subtotals	91	1,704.7	4,433.1	89,129.76	232,700.41	35,354.51
	4	12	242.4	596.0	12,968.60	32,500.00	5,236.58
k = 2	5	18	305.6	831.0	15,799.30	42,544.50	6,062.70
	6a	13	234.2	683.0	12,710.20	37,259.00	4,414.88
	6b	10	178.7	487.0	8,990.80	25,072.00	3,444.45
Light	7a	7	133.5	318.0	6,522.50	16,323.50	2,815.95
	7b	21	379.7	1,046.0	20,444.00	55,758.00	8,049.81
	8a	16	279.8	768.0	13,733.65	38,852.50	5,172.88
	8b	39	543.2	1,982.0	29,559.15	111,311.50	8,353.38
	Subtotals	136	2,297.1	6,711.0	120,728.20	359,621.00	43,550.63
	4	4	62.3	190.0	3,164.80	9,524.00	1,089.57
k = 3	5	15	263.4	787.0	14,734.15	44,187.00	5,019.76
	6a	11	190.2	528.5	9,704.65	26,489.25	3,876.36
	6b	9	141.2	484.0	8,274.95	27,589.50	2,666.28
Moderate	7a	8	124.8	391.0	6,331.35	19,672.50	2,081.36
	7b	12	168.8	558.0	7,949.35	26,703.50	2,626.86
	8a	9	128.6	410.5	5,994.00	19,914.75	1,901.60
	8b	15	227.7	810.5	13,333.30	47,899.75	3,889.21
	Subtotals	83	1,307.0	4,159.5	69,486.55	221,980.25	23,151.00
	4	6	58.5	219.0	2,312.80	9,423.00	722.87
k = 4	5	21	349.7	1,032.0	18,582.30	54,562.50	6,625.95
	6a	31	478.2	1,594.0	25,791.05	88,445.00	8,151.10
	6b	36	432.5	1,740.5	23,372.20	97,436.25	6,152.93
Heavy	7a	24	279.6	1,091.0	14,302.30	55,953.50	4,105.94
	7b	20	197.0	831.5	9,866.30	41,171.75	2,492.94
	8a	21	196.6	841.0	8,678.20	36,808.50	2,318.34
	8b	39	284.3	1,898.0	14,522.35	101,039.50	2,366.11
	Subtotals	198	2,276.4	9,247.0	117,427.50	484,840.00	32,936.18
Grand Totals		508	7,585.2	24,550.6	396,772.01	1,299,141.66	134,992.32

*See text for explanation of symbols and period groups.

TABLE II

BEST FIT VALUES OF THE RATIOS OF Y TO X FOR EACH PERIOD GROUP

Period	n	Negative-Light Class	n	Moderate Class	n	Heavy C'ass
4	32	.413	4	.332	..	.327*
5	35	.387	15	.333	27	.327*
6a	25	.355	10	.332	31	.292
6b	18	.348	9	.300	36	.240
7a	15	.367	8	.322	24	.256
7b	31	.372	12	.298	20	.240
8a	24	.358	9	.301	21	.236
8b	47	.297	15	.278	34	.144

*Periods 4 and 5 combined.

TABLE III

SUMMARY OF ACCEPTED CLASS VALUES OF THE RATIOS OF WEIGHT TO CAPACITY (GMS./CC.)

Classes	n_k	M_k
Negative-Light	227	$0.359 \pm .012$*
Moderate	83	$0.312 \pm .020$
Heavy	198	$0.242 \pm .013$

*95 per cent confidence limits.

TABLE IV

SUMMARY OF CORRELATION COEFFICIENTS AND MEAN STANDARD DEVIATIONS FOR THE COMPLETE SET OF DATA

$r_{yx} : 0.61 \pm 0.06$*	$(S_e)_x : 5.2 \pm .3$*
$r_{yxI} : 0.73 \pm 0.04$	$(S_e)_{xI} : 4.5 \pm .3$
$r_{yxIt} : 0.82 \pm 0.03$	$(S_e)_{xIt} : 3.7 \pm .2$

*95 per cent confidence limits.

THE RELATIONSHIP OF HIGH TEMPERATURES AND LOW RAINFALL TO OYSTER PRODUCTION IN LOUISIANA[1]

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ABSTRACT

The oyster (*Crassostrea virginica*) production (1932-1950) of five parishes of southeast Louisiana were compared with the climatological environmental factors of temperature and rainfall. It was found that when the air temperature was 27.8°C. or over and the rainfall was 7.0 cm. or under for prolonged periods during the preceding summer, there was a significant decrease in the production of oysters the following season. Conversely, it was found that production increased if preceded by a relatively cool-wet summer. From other experimental data which positively correlate to the studies as reported in this paper, it was concluded that the mortalities of oysters occurred during adverse environmental conditions and that it was the mortality rather than the failure to grow that resulted in the decrease of production.

INTRODUCTION

During the course of the biological investigations of the causes of oyster (*Crassostrea virginica*) mortality in Louisiana waters, it was considered necessary to establish the time of year when these mortalities had occurred. This time was established by questioning oyster planters in all sections of the southeastern oyster-producing region of Louisiana. In addition to this, experimental oyster plantings were made and other field experiments were conducted in order that this point might be ascertained. The results of the above procedures showed without exception that the mortalities of planted oysters occurred during the summer months. The experimental data revealed that there was a positive correlation of mortality of oysters with high temperature and high salinity of the water.

As a result of these findings it was decided to ascertain the climatological conditions of past years and then to compare the periods of prolonged high temperatures with the reported production of oysters from the Parishes (counties) of St. Bernard, Plaquemines, Jefferson, La Fourche and Terrebonne. The purpose of this report is to show the relationship of the climatological factors of temperature and rainfall to production of oysters in southeast Louisiana.

[1]Contribution No. 7 from the Contractual Research Program, Division of Oysters and Water Bottoms, Louisiana Department of Wild Life and Fisheries, New Orleans, Louisiana.

The oyster is a poikilothermic organism, the metabolic processes of which are affected by the temperature of its environment. Indirectly, the external temperature controls the life of the oyster in such ways as, (1) determining the solubility of oxygen in water, and (2) affecting the metabolism, population, and behavior of associated organisms, both beneficial and detrimental to the oyster. Dissolved salts in the water play a more subtle role, but like temperature, directly and indirectly, they affect the life of the oyster and associated organisms.

Source of Data

The figures[2] on the production of oysters from the southeastern coastal parishes of Louisiana were obtained from the Division of Oysters and Water Bottoms, which since 1932 has required the reporting of production by the purchaser of market oysters and by the harvester of seed oysters.

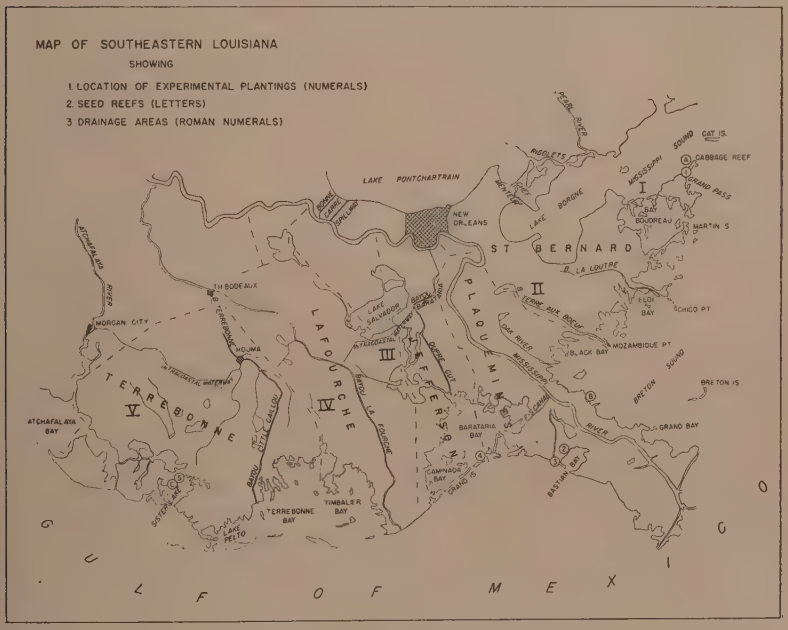

Figure 1.

[2]These figures, in tabular form, are filed in the Marine Laboratory, University of Miami.

The climatological information was secured from the records of the U. S. Weather Bureau.[3] The data on air temperature had been recorded daily, from the following stations: Burwood, Port Sulfur, Buras, Grand Isle and Houma, La., and Bay St. Louis and Gulfport, Miss. From the daily minimum and maximum air temperatures, a daily average was computed for each parish from the weather station closest to the oyster-producing regions of that parish. Weekly averages were computed and the data were then compiled to show the number of consecutive weeks at which the air temperature remained above 27.8°C. No attempt is made to interpolate air temperature to water temperature.

The rainfall data, listed in the Weather Bureau reports as total precipitation in inches or fractions thereof, were compiled in a like manner, and were converted to the metric scale and assembled under the number of consecutive weeks in which the total rainfall did not exceed 7.0 cm.

The number of consecutive weeks in which the air temperature was 27.8°C. or above, and concurrently the rainfall was 7.0 cm. or under, were combined and compared with the figures for production. These results are shown in Figures 2-7.

Interpretation of Data

The question that this study answers is this:—Is there any relation between the production of oysters in Louisiana and the factors of temperature and salinity? Specifically, are the conditions of prolonged drought and hot weather detrimental to oyster production?

The answer to the question lies in the analysis of particular regions which are classified as local drainage areas (Figure 1). Each of the five parishes is located in part or entirely in a certain drainage area. For example, the oysters from St. Bernard Parish were taken from natural beds of the "Louisiana Marsh" region. The ecological conditions of this area (Drainage Area I) differ from those of Jefferson Parish and the western part of Plaquemine Parish, both of which are in Drainage Area III. The production of oysters from the latter area was derived chiefly from the practice of oyster culture. That is, seed oysters were obtained from the natural reefs east of the Mississippi and were transplanted on suitable bedding grounds of Area III. There

[3]Grateful acknowledgement is made to the New Orleans, La., Biloxi, Miss., Gulfport, Miss., and Houma, La., offices of the U. S. Weather Bureau for furnishing published and unpublished data on temperature and rainfall.

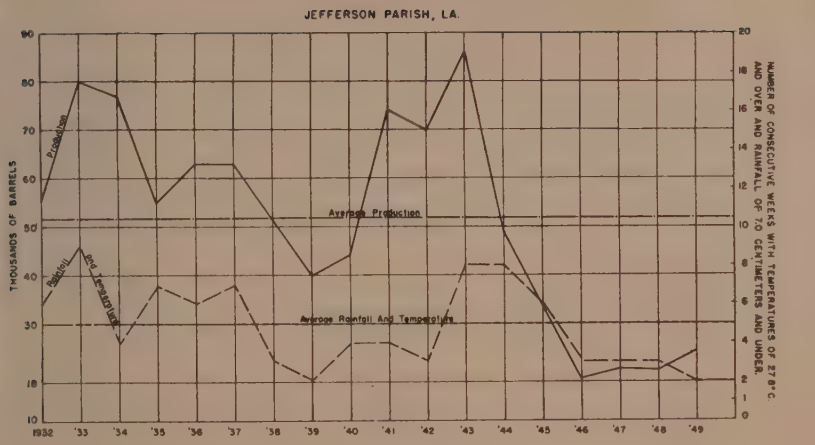
JEFFERSON PARISH, LA.
THOUSANDS OF BARRELS
NUMBER OF CONSECUTIVE WEEKS WITH TEMPERATURES OF 27.8°C AND OVER AND RAINFALL OF 7.0 CENTIMETERS AND UNDER
Production
Rainfall
and Temperature
Average Production
Average Rainfall And Temperature
1932 '33 '34 '35 '36 '37 '38 '39 '40 '41 '42 '43 '44 '45 '46 '47 '48 '49

FIGURE 2.

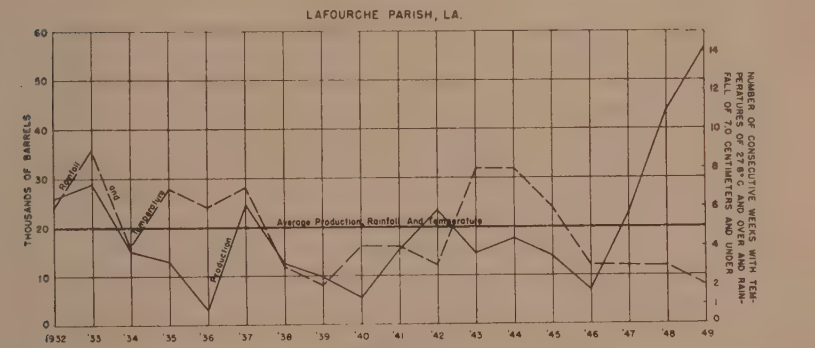
LAFOURCHE PARISH, LA.
THOUSANDS OF BARRELS
NUMBER OF CONSECUTIVE WEEKS WITH TEMPERATURES OF 27.8°C AND OVER AND RAINFALL OF 7.0 CENTIMETERS AND UNDER
Rainfall
and
Temperature
Production
Average Production, Rainfall And Temperature
1932 '33 '34 '35 '36 '37 '38 '39 '40 '41 '42 '43 '44 '45 '46 '47 '48 '49

FIGURE 3.

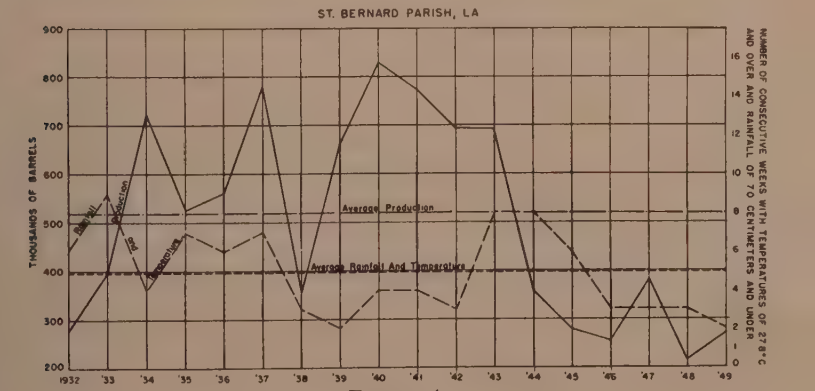
ST. BERNARD PARISH, LA
THOUSANDS OF BARRELS
NUMBER OF CONSECUTIVE WEEKS WITH TEMPERATURES OF 27.8°C AND OVER AND RAINFALL OF 7.0 CENTIMETERS AND UNDER
Rainfall
and
Temperature
Production
Average Production
Average Rainfall And Temperature
1932 '33 '34 '35 '36 '37 '38 '39 '40 '41 '42 '43 '44 '45 '46 '47 '48 '49

FIGURE 4.

are no productive natural reefs in the southern extremities of Areas III and IV. Areas I, II and V are subject to cyclic fluctuations in salinity as a result of the periodic high water discharge of the Pearl, Mississippi and Atchafalaya Rivers, respectively. Thus, a third factor is introduced which interacts with the factors of high temperature and salinity as influenced by local rainfall. This will be discussed in a separate report.

The life cycle of the oyster must be considered in order that an intelligent interpretation be made of these data. In the southeastern region of Louisiana, oysters spawn in the late spring and continue throughout the summer months. The young oysters grow rapidly, depending, of course, on many environmental factors. The juveniles of a population are not as susceptible to the vicissitudes of the environment as are the adults, the latter being classified by length of 70 mm. or over. The age of an oyster is relative, depending on many factors of the environment plus the adaptative genetic potential of the individual. The young oysters generally survive their first summer either on the natural reef or as transplanted stock regardless of the temperature or salinity, provided that maximum extremes are not reached. The rapid growth of Louisiana oysters results in a marketable product within 12 to 18 months in most areas of Louisiana. It is the interaction between the factors of growth and mortality that determines the production (Hopkins and Menzel, 1952). The data in this report shows that prolonged periods of high temperature and low rainfall affect the production of oysters as reported for the year or years following the hot-dry period. The prolonged periods of an adverse hot, dry environment could affect production by (1) retarding spawning or setting or both, (2) retarding growth, (3) being a direct or indirect mortality factor. Any one of these effects, or combinations of them, is reflected in the production of the following fall-winter season. Other climatological factors such as an optimum climate during the spring, winter or fall, would undoubtedly tend to offset the detrimental effects of a severely adverse summer. Other environmental factors such as the amount of fresh water from the rivers would also tend to nullify the detrimental effects of adverse summers. To repeat, the temperature and salinity are factors which affect growth and mortality, which in turn determine the production.

The graph of the production of Jefferson Parish (Figure 2), shows a positive correlation between production and duration of periods of high temperature and low rainfall. The distance from any source of

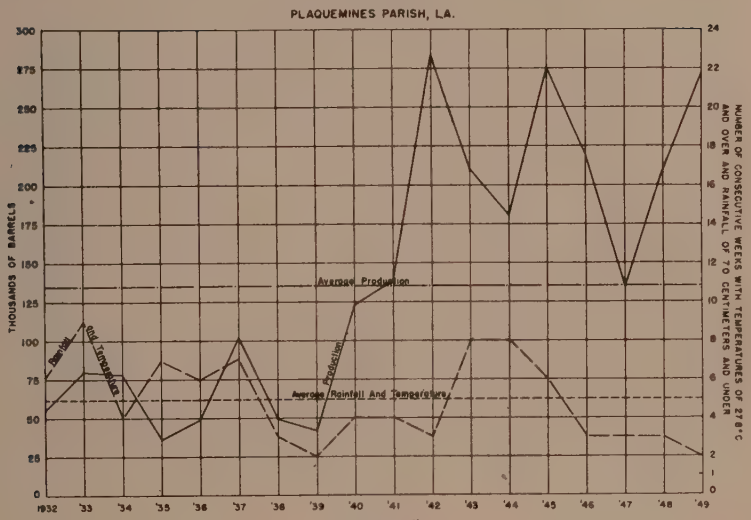
PLAQUEMINES PARISH, LA.
THOUSANDS OF BARRELS
NUMBER OF CONSECUTIVE WEEKS WITH TEMPERATURES OF 27.8°C AND OVER AND RAINFALL OF 7.0 CENTIMETERS AND UNDER
Average Production
Average Rainfall And Temperature
Rainfall
Old Temperature
Production
1932 '33 '34 '35 '36 '37 '38 '39 '40 '41 '42 '43 '44 '45 '46 '47 '48 '49

FIGURE 5.

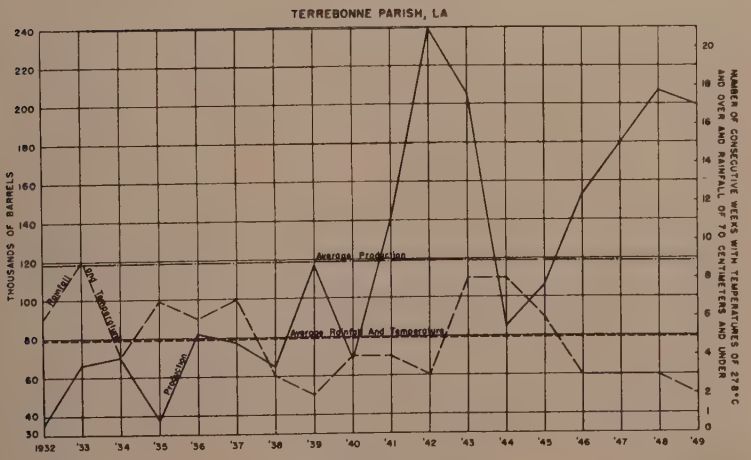
TERREBONNE PARISH, LA
THOUSANDS OF BARRELS
NUMBER OF CONSECUTIVE WEEKS WITH TEMPERATURES OF 27.8°C AND OVER AND RAINFALL OF 7.0 CENTIMETERS AND UNDER
Average Production
Average Rainfall And Temperature
Rainfall
Old Temperature
Production
1932 '33 '34 '35 '36 '37 '38 '39 '40 '41 '42 '43 '44 '45 '46 '47 '48 '49

FIGURE 6.

fresh river water drainage undoubtedly accounts for this. Referring to Figure 2, when there were prolonged periods of high temperature and low rainfall during the summer of 1933, there was a decrease in production the following year, and production continued to decrease until 1935. In 1934, there was less than one-half the number of consecutive weeks of high temperature and low rainfall than in the previous summer. This is reflected in the increase during the 1935-1936 seasons. The summers of 1935, 1936 and 1937, had 7, 6 and 7 consecutive weeks of drought and high temperatures, respectively. The result of this was a decrease in production in 1938, the lowest production until 1946. The summers of 1938, 1939, 1940, 1941 and 1942, were optimum periods for the environmental factors of temperature and rainfall. A corresponding production rise between 1939 and 1940 culminated in the peak production record of 1943, and this occurred during a period of labor shortage as a result of the national emergency of that period. The 8 weeks of high temperature which occurred in 1943 resulted in a decline in the production in 1944. Although not as severe as the two preceding summers, the less severe conditions of the summer of 1945 did not check the declining production. The years 1946-1947, periods of optimum summers, brought about a leveling off in the decline of production and a slight increase in 1947 and 1948. The production curve shows a slight increase between 1948 and 1949, as a result of the optimum conditions of the past summers. Biologically, it appears that the population had decreased to a critical point, one that would require several years of optimum conditions in order that rehabilitation might ensue and the population be increased to numbers where fluctuations might be observed. The sharp increase in production in 1950 attests to the above generalization.[4]

The production curve and the temperature-rainfall curve of La-Fourche Parish (Figure 3) show the same trend, although not as conclusively as Jefferson. Nine weeks of high temperature and low rainfall in 1933 correlate with the decreased production of 1934, which was an optimum summer correlating with the recovery in production of 1935. The summers of 1935 and 1936, produced detrimental conditions which resulted in a loss in production in 1936. There is a negative correlation between the climate of 1936 and the production of 1937, which year in Louisiana was the fifth highest in total pro-

[4]Data obtained by personal communication from Division of Oysters and Water Bottoms, Department of Wild Life & Fisheries, New Orleans, La.

duction of the last 21 years (Figure 7). The adverse conditions resulting from high temperature and drought could have been rectified by the flood waters from the Mississippi River in 1935, and the Mississippi and Atchafalaya Rivers in 1937. There is again a negative correlation in 1938 and 1939 following the positive correlation of the summer of 1937. Extremely low production was common to all of the parishes in 1938 following the flood in 1937. The nearly average climatological conditions of 1940, which were duplicated in 1941, resulted in a rise in production in 1941 and 1942. The conditions of 1943, a year of high water and floods, duplicated the year 1937 (Figure 8). The adverse summer environmental conditions of 1943, 1944 and 1945, resulted in the low production of 1946. In 1946, 1947, 1948 and 1949, optimum conditions of temperature and rainfall prevailed and are reflected in the sharp and steady rise in production from 1947 through 1950. Concurrent with the optimum climatological factors, the fresh water discharge from the rivers was also optimum, which fact undoubtedly accounts for the increased production of 1949 (Figure 8).

An analysis of the graphs (Figures 4, 5 and 6) of the parishes of St. Bernard, Plaquemine and Terrebonne, shows similar relationships, though not as significant as those of Jefferson and La Fourche Parishes. The production of east Plaquemine and St. Bernard has been controlled chiefly by the amount of fresh water discharged from the Mississippi and Pearl Rivers. The Atchafalaya River, the third largest river (in volume discharged) of the United States, during periods of low water discharge, has increasingly become a major production-controlling factor for Terrebonne Parish (Area V).

An analysis of the graph which compares the total Louisiana production with the number of consecutive weeks of high temperature and low rainfall (Figure 7) shows that the high production periods of the past 12 years have followed periods of one month or less of drought and continuing heat. Conversely, the peak of production of 1942 fell sharply to a critical low, following the two-month periods in each of the two years, 1943 and 1944.

Conclusions

The results of this study show the effects of the type of summer on the production of oysters the following seasons. No conclusions can be drawn *per se,* but the climatological conditions can be connected to

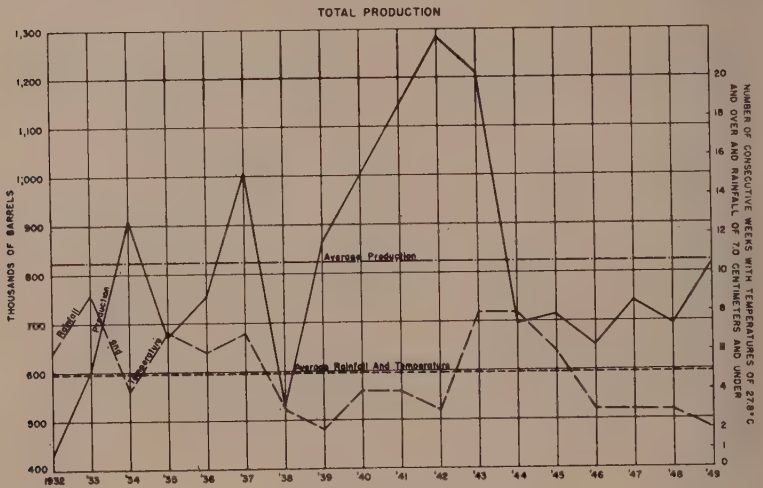
TOTAL PRODUCTION
THOUSANDS OF BARRELS
NUMBER OF CONSECUTIVE WEEKS WITH TEMPERATURES OF 27.8°C AND OVER AND RAINFALL OF .10 CENTIMETERS AND UNDER
Average Production
Average Rainfall And Temperature
Rainfall Production And Temperature

FIGURE 7.

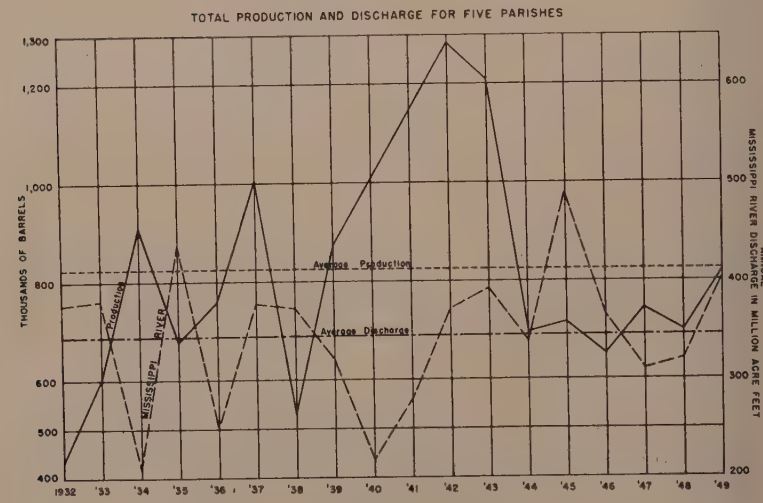

FIGURE 8.

the previously collected experimental data and to the information derived from oyster planters. The accumulated information shows conclusively that mortality of oysters was the primary reason for the low production of certain years. These excessive mortalities occurred during the periods of prolonged high temperature and high salinity of the water.

REFERENCE

HOPKINS, S. H. AND R. W. MENZEL
1952. How to decide the best time to harvest oyster crops. Atlantic Fisherman, *33* (9): 15, 36-37.

GROWTH AND MORTALITY OF OYSTERS IN LOUISIANA[1]

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The University of the South, Sewanee, Tennessee

ABSTRACT

Experimental plantings of seed oysters (*Crassostrea virginica*) were made at five locations in the oyster-producing area of southeastern Louisiana. The results which were obtained showed that the yield of planted oysters is determined by the inter-action between the growth factors and the mortality factors of the environment. It was found that undue mortalities occurred in certain areas of normally rapid growth in 1947-48.

INTRODUCTION

During the extensive investigations on the causes of oyster mortalities in Louisiana coastal waters, it seemed essential to derive a practical definition for "undue mortalities," which would be understood by both the oyster biologist and the oyster planter. The oyster biologist has been inclined to calculate mortality of oysters in terms of individuals, expressed as the per cent living and dead, whereas the oyster planter computes his mortalities in terms of gross loss, *i.e.*, losses in bushels, sacks or boatloads, or in other words, in terms of yield. It also seemed desirable to determine whether or not undue mortalities occurred at selected locations. This information was derived from experimentation and a mathematical analysis of our results.

Oyster culture in Louisiana generally consists of obtaining seed oysters from a natural reef and planting them on a suitable bottom until they grow to "market-size" (a length of 75 mm. or over). The oyster planter calculates his yield in terms of the volume of seed oysters planted. For example, if an oysterman plants 1000 sacks of seed oysters and harvests 1000 sacks of market oysters, his yield in terms of a ratio is 1:1. A 1:1 yield may be economically profitable. To produce this yield, two factors, growth and mortality, have been operating. These two factors are counteracting, and it is essential to know their relationship in order to give a more practical meaning to a mortality investigation.

[1]Contribution No. 8 from the Contractual Research Program, Division of Oysters and Water Bottoms, Louisiana Department of Wild Life and Fisheries.

The method of handling data to show the relationship between growth and mortality of oysters was used originally by Dr. S. H. Hopkins, and full acknowledgement is made of his contribution, which has been adapted to the experimental data reported herein (Hopkins and Menzel, 1952).

Methods

Experimental plantings of seed oysters were made at five locations in the oyster-producing area of southeastern Louisiana (Figure 1). Louisiana oystermen and gear were hired for the operation. The procuring of seed and the bedding of oysters was consistent with the current practice of oyster culture in Louisiana.

At each location a hard bottom was selected, and all live oysters were removed. A rectangular area of 150 feet by 50 feet was planted

Figure 1.

TABLE II

AVERAGES FROM THE INDIVIDUAL SAMPLES OF THE LENGTH, NUMBER PER BUSHEL, AND MORTALITY OF OYSTERS.

Number and Location of Experimental Station	Date of Sampling	No. of Samples	Average Length in mm.	% Mort. per Sample	Number of Oysters per Bushel
1	xi- 4-47	7	47.7	6.4	2100
	i-15-48	3	66.6	8.7	1250
Grand Pass	v- 4-48	3	61.3	23.5	950
	vi-29-48	3	62.5	19.7	950
	x- 6-48	3	73.5	40.2	600
	xi-24-47	6	55.6	10.9	1250
2	i-27-48	3	60.3	15.3	1050
	iv-29-48	3	67.7	74.2	750
Upper Bastian Bay	vi-30-48	3	——	100.0	——
	xi-20-47	7	55.4	10.5	1250
3	i-29-48	3	65.4	71.9	850
	iv-29-48	3	80.0	83.3	450
Lower Bastian Bay	vi-30-48	3	——	100.0	——
	xii- 2-47	6	60.0	10.8	1050
4	i-28-48	3	64.2	31.0	900
	iv-29-48	3	79.3	51.9	500
Independence Isle	vi-30-48	3	82.2	70.1	450
Barataria Bay	x-13-48	1	84.3	76.2	400
	xii-16-47	8	52.6	6.5	1500
5	iv- 6-48	3	55.5	9.7	1250
Sister Lake					

with 225 sacks (one sack = 1½ U. S. Standard Bushels) of seed oysters. The seed oysters were rough culled, allowed to dry partially, and then were marked with paint, which by previous experimentation was found to be a satisfactory method of marking oysters. The experimental plantings were made between November 4, and December 17, 1948. Representative ½ bushels (½ U. S. Standard Bushel) of seed oysters were sampled for mortality by separating the live oysters from the dead individuals—a dead oyster being two halves which are held together by the hinge ligament, forming an "intact box." Each oyster of the sample was measured for length with Vernier calipers, the distance between the umbo and the most distant part of the bill constituting the length. The number of oysters both dead and alive in the sample was determined by actual count. On subsequent examinations of the experimental plots, the oysters were collected by tongs and the same procedures were followed, using only marked oysters.

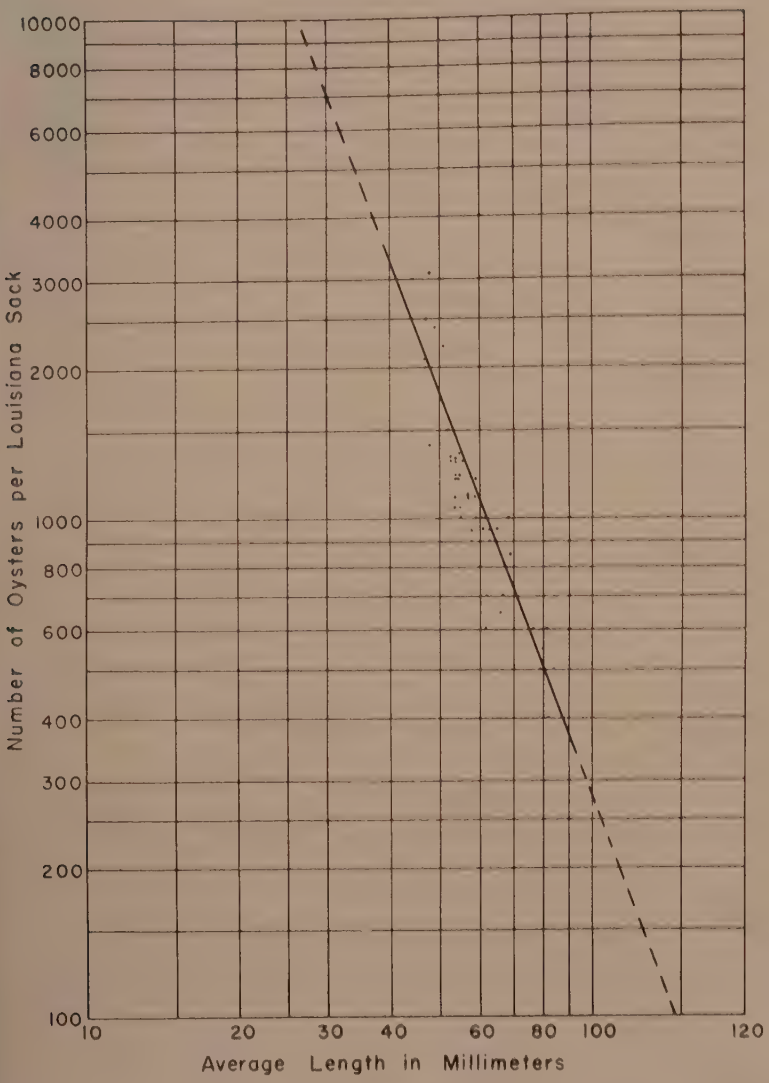
10000
8000
6000
4000
3000
2000
1000
800
600
400
300
200
100
Number of Oysters per Louisiana Sock
10
20
30
40
60
80
100
120
Average Length in Millimeters

FIGURE 2.

Results

From the average length of oysters from the individual samples and the number of oysters per sack,[2] a logarithmic graph was plotted which shows the relationship between the average length of oysters and the number of oysters per sack (Figure 2). Table II shows the averages of the individual samples, number per bushel, and the percentage mortality which was computed from counts of "intact boxes."

Table III was constructed from Figure 2. This table shows the potential yield resulting from growth if no losses occur. If mortality or losses occur, Table IV can be used to determine the expected or natural mortality which will occur to produce a 1:1 yield. Table II and Figures 3 through 7 show the comparative results of the rates of mortality and growth at the selected experimental locations under the time and conditions of the experimental plantings. The expected mor-

TABLE III

Yield resulting from growth of seed oysters (average length expressed in rounded figures in millimeters). The yield is the number of sacks harvested for each sack planted, assuming no loss occurs. Computed from data shown in Figure 2.

Initial Length in mm.	Average Length in mm. When Harvested								
	45	50	55	60	65	70	75	80	85
45	1.0	1.27	1.62	2.04	2.58	3.26	4.12	5.22	6.71
50	—	1.0	1.27	1.61	2.03	2.57	3.25	4.11	5.21
55	—	—	1.0	1.27	1.61	2.03	2.56	3.25	4.10
60	—	—	—	1.0	1.25	1.60	2.01	2.55	3.24

TABLE IV

Expected mortality or losses in percent resulting in a 1:1 yield. The average length is expressed in rounded figures in millimeters, the vertical column being seed oysters and the horizontal the length when harvested.

Initial Length in mm.	Final Length of Oysters Harvested								
	45	50	55	60	65	70	75	80	85
45	0%	21.3%	37.9%	51.0%	61.2%	69.3%	75.7%	80.8%	85.1%
50	—	0%	21.6%	37.8%	50.8%	61.0%	69.1%	75.5%	80.6%
55	—	—	0%	21.5%	37.5%	50.5%	60.8%	68.9%	75.3%
60	—	—	—	0%	21.3%	37.3%	50.2%	60.5%	68.7%

[2]These data are contained in Table I, filed at the Marine Laboratory, University of Miami.

talities essential to give a 1:1 yield based on measured growth rates are shown by a broken line.

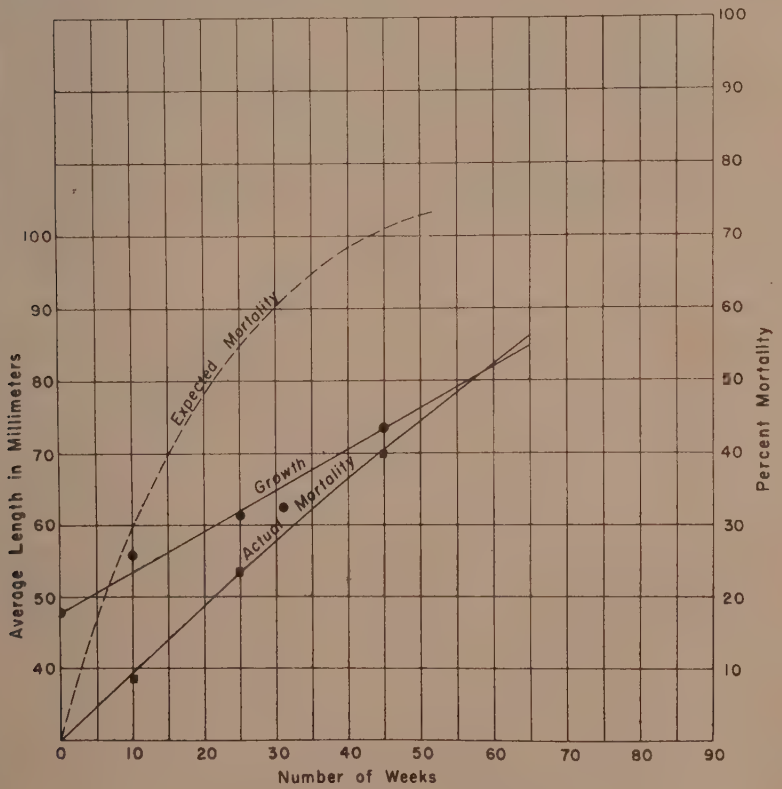

FIGURE 3. Station 1, Grand Pass.

DISCUSSION

The results which have been obtained in this investigation are of practical importance to both the oyster grower and the oyster biologist. For example, as shown in Table III, if an oyster planter beds 50 mm. seed oysters and harvests 75 mm. market oysters, he will obtain 3¼ sacks for every sack planted if no losses occurred. If this seed had been planted at Station 1, it would have taken approximately 11 months under the conditions of 1947-48 to obtain market-sized

oysters. At Station 3, the same seed would have grown to market size (75 mm.) in approximately 5-6 months from the time of the late fall planting. The Sister Lake (Station 5) oysters practically had reached their limit of growth at the time of the planting in this particular ecological location.

The practical value of this data is known to oystermen; they know from experience which locations are best for rapid growth. Even in areas of rapid growth, few oystermen expect to harvest 3¼ sacks for every sack of 50mm. seed planted. Some oystermen find it economically profitable to get a return of one sack for every sack of seed

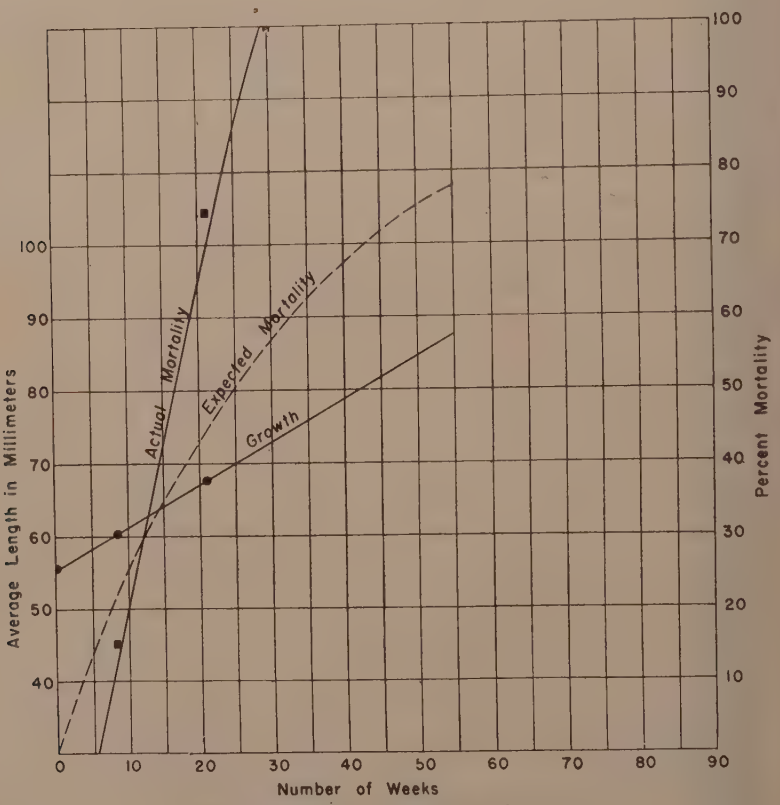

FIGURE 4. Station 2, Upper Bastian Bay.

oysters planted, as applied for the yield examples in this paper. In order to obtain a 1:1 return, growth must counteract mortality (Table IV).

The percentage mortality derived by many oyster biologists, which is computed from individuals, can give an erroneous picture unless interpreted with the natural or expected mortality of a given area. For example, at Station 1 the actual mortality in October was 40%. The expected mortality, based on growth for a 1:1 yield was computed to be 70% (Figure 3). The actual mortality, although it appears high, shows that there would not have been a net loss from the operation.

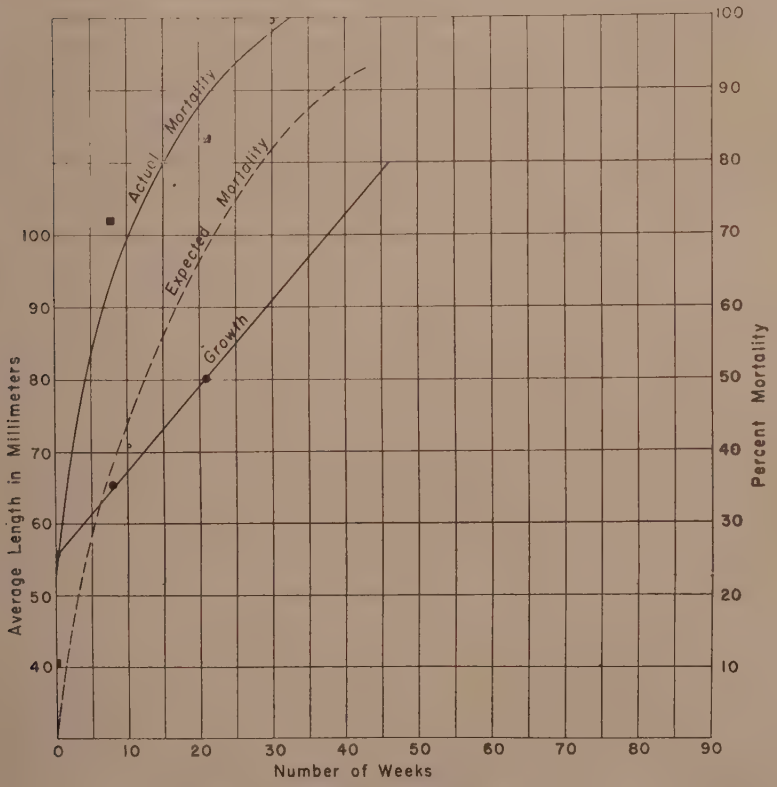

FIGURE 5. Station 3, Lower Bastian Bay.

In fact, the net gain would be greater than a 1:1 yield. On the other hand, in Lower Bastian Bay, when the individual loss exceeded the expected loss in April, it was suspected that other factors which were described as "unknown causes which produced undue mortalities" were operating. This was conclusively proven in June, when after careful searching, not a single live oyster could be found (Figures 4, 5). The individual percentage mortality of the Barataria plantings was 51% in April. Based on the growth factor essential for a 1:1 yield, this approximated the expected mortality of 59%. During May and June, however, mortalities occurred which were not counteracted by growth; the mortality based on individuals was 70%, whereas 61%

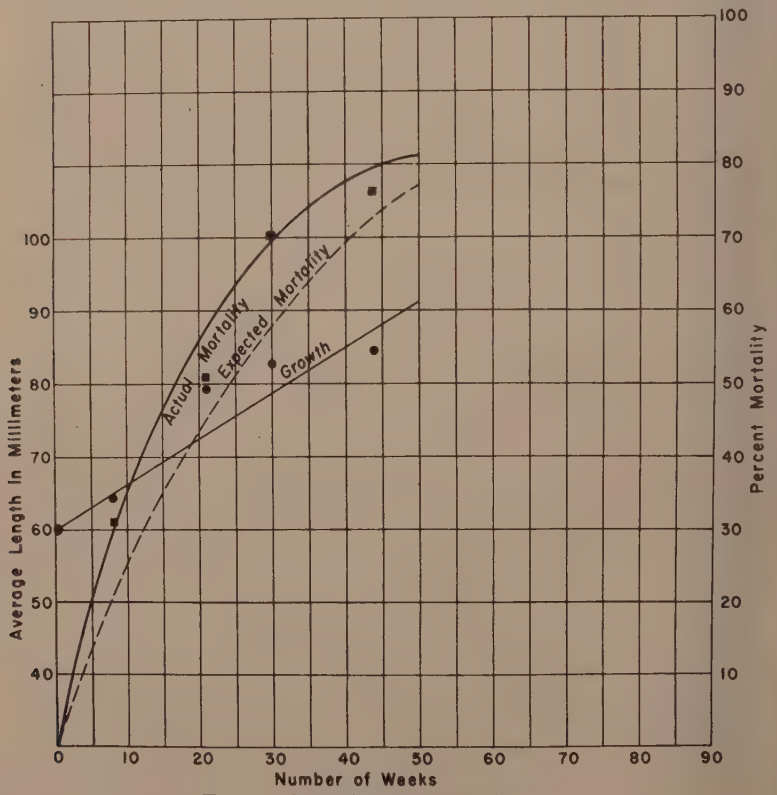

FIGURE 6. Station 4, Barataria Bay.

was expected. The remainder of the summer produced a continued increase in mortality which was not compensated by growth, the result being that a harvesting operation would have resulted in a yield less than 1:1 (Figure 6).

From the results of this experiment it has been found that Bastian Bay is an area of rapid growth and high mortality. To a lesser extent, the same is true of lower Barataria Bay. Generally, this is what is expected by experienced planters and, if intelligently exploited, such an area could be a profitable area. It ceases to be profitable when the mortality factor exceeds the growth factor. The present practice of

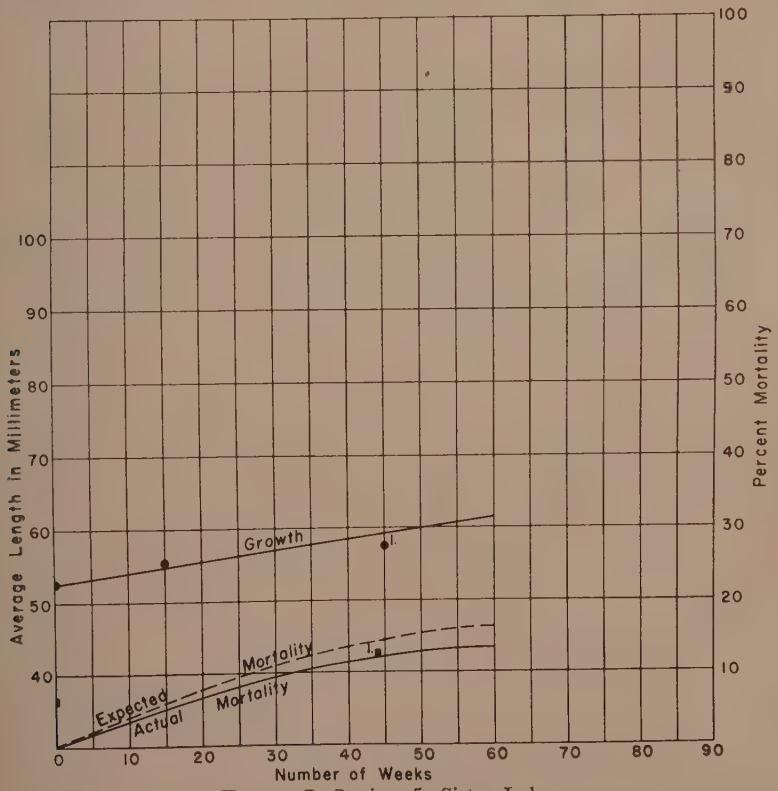

FIGURE 7. Station 5, Sister Lake.

progressive planters in the southern extremities of Barataria and Bastian Bays has been to plant large seed oysters in the late fall and harvest them before the following summer. Our data confirms the wisdom of this practice.

The results that have been obtained from the experimental plantings have shown that the growth rate is an integral part of a biological mortality problem, and confirms the results of the plantings of Hopkins and Menzel (1952). The mortality percentages which are based on individuals become of practical importance when they are balanced against growth rate in known periods of time and interpreted in terms of yield.

Conclusions

The interaction between the growth factor and the mortality factor determines the yield of planted oysters.

During the optimum growing period, the rate of mortality and growth was found to be greater in Bastian Bay and Lower Barataria Bay than at Grand Pass and Sister Lake.

The actual mortality rate exceeded the expected mortality, which is based on growth necessary for a 1:1 yield at Bastian Bay and to a lesser extent in lower Barataria Bay; therefore, undue mortalities occurred in the planting operations in these areas in 1947-48.

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INTERTIDAL EROSION ON THE FLORIDA KEYS[1]

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ABSTRACT

Intense erosion of calcareous shore rocks in the coral seas produces a thoroughly honeycombed, brittle rock. Examples of this erosion on the Florida Keys are described. Physio-chemical solution of calcium carbonate is considered only of local importance in intertidal erosion. It is suggested that the activities of boring and burrowing organisms are a major factor in this erosion.

INTRODUCTION

Calcareous rocks exposed between the tide marks in the coral seas are much affected by destructive processes commonly termed intertidal erosion. As shown in Figures 2-5, and in numerous plates in the literature of the coral seas, rock is so thoroughly dissected that it is often difficult to cross on foot. Sharp pinnacles and projections whose dimensions vary from a few inches to a foot or more alternate with all manner of irregular cavities and passageways of similar dimensions.

This thorough-going erosion produces a sponge-like network of rock which retains, at low tide, only a relatively small amount of water in pits and depressions. A notch at approximately the mid-tide level is often present on the exposed face of shores where the limestone extends a few feet above the high water mark.

Elevated reefrock, cemented reef rubble and beachrock are the most common shore rocks which show intertidal erosion. Whatever the rock, it is superficially hardened, and discolored in shades of black, gray, yellow and brown.

Few works which consider the problems of the coral seas have failed to describe and discuss intertidal erosion. Representative descriptions and discussions may be found in Agassiz (1894, 1896), Gardiner (1903), Kuenen (1933), and Fairbridge (1948).

This paper briefly describes intertidal erosion in Southeast Florida and presents observations which suggest that boring, burrowing and

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browsing organisms make an important contribution to this erosion.

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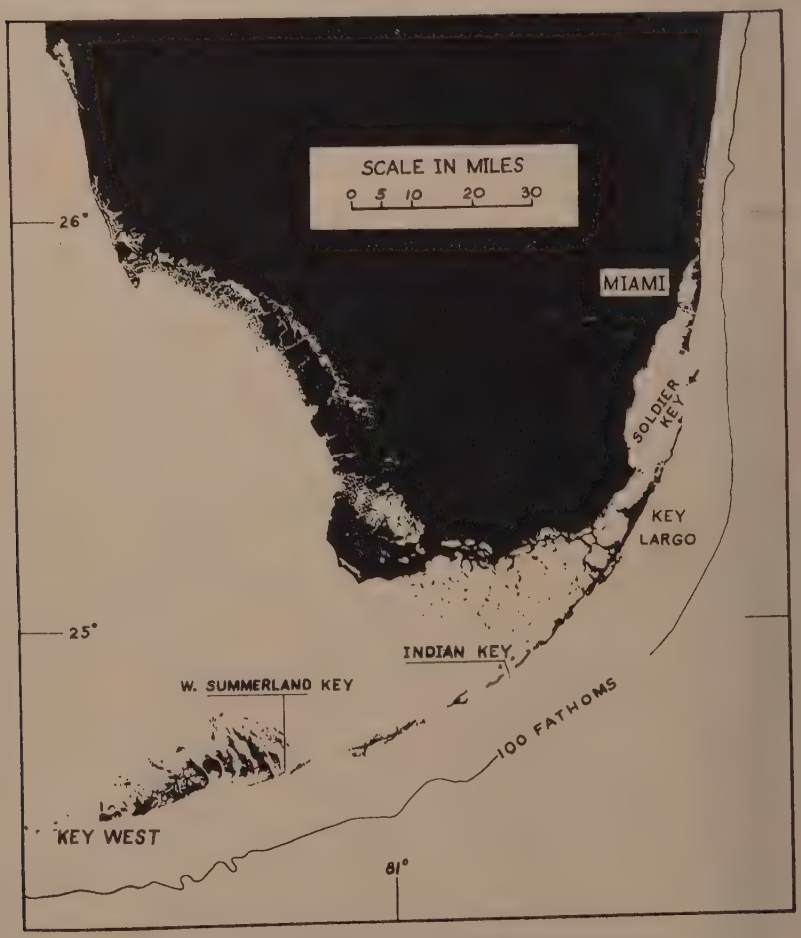

FIGURE 1. South Florida and The Florida Keys.

identified the organisms. An earlier version of the manuscript was read by Rhodes W. Fairbridge and K. O. Emery.

Intertidal Erosion in Southeast Florida

Intertidal erosion is well shown on the rocky shores of the Florida Keys from Soldier Key, off Miami, to Key West, and on a few keys between Key West and the Dry Tortugas (see Figure 1). The Key Largo limestone, a Pleistocene coral reef, forms the rocky shores which alternate with mangrove swamps and beaches between Soldier Key and Key West. Beachrock is exposed on the shores of Loggerhead Key in the Dry Tortugas, and between there and Key West a few rocky shores of Miami Oölite may be seen.

Between Soldier Key and Key West, where the mean tidal range is 1.9 feet on the ocean or southeastern side of the keys, most of the

Figure 2. Intertidal zone of Indian Key showing lower platform and dissected margin of upper platform with undercutting.

rocky shores consist of an upper and lower platform separated by two feet or less (Stephenson and Stephenson, 1950; see Figure 2). The upper platform, which ranges in width from a few feet to some fifty feet, is discolored by surface growths of organisms in bands parallel to the shore, and Stephenson and Stephenson (1950, p. 396) recognize a white, black, and yellow zone related to tide levels: "The level of high water of spring tides varies on different days and in different weathers. At the higher springs the black zone is covered or wetted and the grey zone less so, though its seaward parts may be at least invaded. The white zone appears to be wetted only exceptionally when tide and weather combine to raise the level higher than usual. The yellow zone is regularly intertidal."

The white zone is unaffected by intertidal erosion and consists of a series of smooth rounded domes and basins formed by a thin lithified laminite overlying the Key Largo limestone. The black zone extends from two to two and one-half feet above the level of low water springs (Stephenson and Stephenson, 1950), and is generally less than ten feet in width. The yellow zone forms the outer margin of the black and extends down to the lower platform.

All the rock between the lower platform and the top of the black zone shows the effects of intertidal erosion, and the dissection is most intense in the irregular yellow zone, as shown in Figure 2.

At several localities, as on Indian Key, West Summerland Key and Key Largo, the boundary between the upper and lower platforms, the yellow zone, is deeply dissected and fissured so much so that residual pinnacles and table like masses supported by narrow columns are produced. In some cases these are preserved as isolated remnants of the former extension of the upper platform, as at the upper left of Figure 2. Undercutting is common as shown in Figures 2 and 4.

Elsewhere the upper platform is reduced to a few feet in width and a thickness of three to four feet of Key Largo limestone is exposed to erosion (Figure 4). Here undercutting is prominent and extensive. Examples of this type of shore can be seen on Indian Key, Key Largo Sound and the bay side of Key Vaca.

All the rock affected by intertidal erosion has a superficial hardening to a depth of a half-inch or less. In thin section, this crust is found to be thoroughly cemented by a fine-grained, clear, calcite mosaic which is indistinguishable from the cement of the subaerially exposed Key Largo limestone. Beachrock shows the same acicular aragonitic

cement on the hardened surface, as can be seen internally (Ginsburg, 1953).

A few chemical analyses (Tayama, 1952, p. 216; Vaughan, 1918, p. 288) indicate that the eroded rock has a higher magnesium concentration than unaffected material.

Explanations of Intertidal Erosion

Physico-chemical Solution

Physico-chemical solution of calcium carbonate by sea water in the intertidal zone has been considered to be the primary cause of intertidal erosion by Kuenen (1933, 1950). Fairbridge (1948) suggested that the increased solubility of carbon dioxide in the cooler water of the evening and the absence of algal uptake of this gas is responsible for solution. Gardiner (1903), Fairbridge (1948), Macfayden (1930) and others have called attention to the boring and burrowing action of organisms as a biological contribution to intertidal erosion. Gardiner (1903, p. 34) called attention to the hardening of exposed rock in the intertidal zone by precipitation of calcium carbonate. Agassiz (1894) and Gardiner (1903) suggested that rain and sea spray are important erosive agents.

Emery (1946) has studied a special type of intertidal erosion in California. He found that the shallow basins of the intertidal zone were due to solution of the calcite cement of the shore sandstone. Solution of calcite was demonstrated during the nocturnal low tide isolation of the basins as a result of organic respiration unbalanced by algal uptake of carbon dioxide. This type of solution is also to be expected in interstitial and surface films of water remaining on the rock at low tide. However, as erosion of vertical surfaces, which retain less seawater than horizontal portions or depressions, is as intense, if not more, than the attack on horizontal surfaces, this type of solution is probably of relatively minor importance. Furthermore the precipitation occurring during the daytime isolation of pools, which Emery (1946, p. 226) considers so loosely attached to the rock that it can be removed by wave action, may instead occur as an interstitial cement giving the rock its characteristic surficial hardness. It is also probable that the precipitation of calcium carbonate in isolated pools or films of seawater in the tropics, where daytime evaporation and heating are intense, exceeds by a considerable amount any nocturnal solution.

Two other lines of evidence suggest that solution by intertidal seawater is unlikely. Firstly, aragonite is about 1.5 times more soluble than calcite, yet no selective solution of aragonite was found in beachrock showing intertidal erosion[2]. Secondly, if aqueous solution were important in the intertidal zone, one would expect the rock to be weak and chalky, but instead it shows a superficial hardening as a result of precipitation of calcium carbonate.

Kuenen (1950) suggested that humic acids from decaying vegetation, wave pressure, and rain water may also cause physico-chemical solution.

In many cases the acids developed in decaying vegetative debris are attacking calcareous rocks, as in the case of acid mangrove peat on limestone, but there are numerous examples of intertidal erosion on islands with little or no vegetation or organic soils.

It is not clear just what effect the pressure of waves is thought to have on the calcium carbonate-carbon dioxide-water equilibrium; certainly the pressure effect on the dissociation constants is of no great importance.

If one takes the solubility of calcium carbonate in rain water at 25° to be 0.044 gr./L. (Miller, 1952, p. 195) and a rainfall of 150 cm./yr., 66 gr. or 24.1 $cm.^3$ of calcite could be dissolved from a square meter of calcareous rock in one year. For the intertidal zone, which is exposed half the time, this figure should be divided by two. The possible solution of 12.05 $cm.^3$ of calcite from a square meter of rock surface would mean a lowering of the surface of 0.0012 cm./yr., which in the author's view is a relatively trivial portion of the probable total effects of marine erosion. Moreover, the solution of calcium carbonate requires that the undiluted rain water remain in contact with the rock long enough to become saturated, and such conditions are not fulfilled in the honeycombed rock of the intertidal zone.

The preceding discussion indicates that physico-chemical solution is probably not the most important process of intertidal erosion, and therefore the biological erosive agents were examined to assess their importance.

Boring and Burrowing Organisms in the Intertidal Zone

Several investigators have called attention to the rock destroying and weakening activities of intertidal organisms. Gardiner (1903, pp.

[2]Beachrock has the same percentage of aragonite as the unconsolidated beachsands (Ginsburg, 1953).

335-338) treated the boring fauna and flora from the Maldive and Laccadive archipeligoes. Otter (1937) discussed the boring animals collected and observed during the Great Barrier Reef Expedition. Fairbridge (1948) called attention to boring animals as agents of erosion. Kühnelt (1950) describes the boring mechanisms of the major animals of the intertidal zone. Duerden (1902) recognized the boring algae as perhaps the most important agent in the disintegration of calcareous material in the tropics.

Boring and Burrowing Animals in the Intertidal Zone. The following list of organisms from the intertidal zone in Florida is based on general collections and observations by the author's colleagues.

I. Forms which penetrate the rock:
   Phylum Porifera
      Family Clionidae
   Phylum Annelida, Class Gephyrea, Order Sipunculoidea
      Physcosoma antillarum
      Physcosoma varians
      Aspidosiphon speciosus
   Phylum Arthropoda, Class Crustacea, Order Cirripedia
      Lithotrya dorsalis

II. Forms which have exposed, generally shallow burrows:
   Phylum Mollusca, Class Pelecypoda
      Arca barbata
      Mytilus (Brachidontes) exustus
   Phylum Mollusca, Class Amphineura
      Acanthopleura granulata
   Phylum Echinodermata, Class Echinoidea
      Echinometra lucunter

III. Grazing forms:
   Phylum Mollusca, Class Gastropoda
      Hipponix antiquata
      Siphonaria spp.
      Littorina spp.
      Nerita spp.
   Phylum Mollusca, Class Amphineura
      Acanthopleura granulata

FIGURE 3. Intertidal erosion of beachrock on Loggerhead Key, Dry Tortugas.

The faunal list is by no means complete and extensive collection will certainly produce many more forms.

I. Several specimens of a stalked boring barnacle, *Lithotrya dorsalis,* have been collected, and at one locality, Indian Key, they were abundant. The sipunculoids are abundant in that portion of the intertidal zone where the rocks are usually covered with an algal mat. The bores are a few millimeters in diameter and several centimeters in length. Boring sponges are very common in this zone below the algal mat.

II. *Arca* is found almost buried in the rock, and Otter (1937, p. 328-9) considers it an active borer. The hoof shell, *Hipponix,* is a questionable borer; Fisher (1950, p. 132) places it with *Patella* as excavating shallow depressions in the rock with its foot. Chitons occupy depressions in the intertidal zone. The faeces of the local species are calcareous, as was the case with those col-

lected during the Barrier Reef Expedition (Otter 1937, p. 332). Rasping with the radula is the mode of excavation. *Echinometra lucunter* has not been found out of water at normal low tide. It occupies roughly spherical cavities and can only be removed by breaking the rock. Otter (1937, p. 333) has reviewed the literature on the mode of excavation; it is thought to be a combination of the pick-like action of the teeth and abrasion by rotation of the spines. *Brachidontes* is extremely abundant locally and often covers rock surfaces completely in the intertidal zone (see Figure 8). It is a byssus-attached form which is generally attached with its long dimension perpendicular to the rock surface. Commonly the umbo projects into the rock several millimeters. The manner in which these pits are produced is not known.

III. The several grazing forms of the intertidal zone remove loose rock particles as they rasp the surfaces for food.

The cumulative effect of the organisms discussed above is threefold: (1) Borers which penetrate actually remove calcareous material and weaken the rock such that wave action can remove fragments. (2) Forms which excavate shallow depressions remove material and provide a more suitable environment for algae. (3) Borers increase the surface area of a given rock volume and thus provide more space for surficial forms such as the boring algae discussed below.

Boring Algae. The existance of several species of green and blue-green marine algae which bore into calcareous material has been known for many years. Bornet and Flahoult first called attention to some of these forms in 1889. Nadson (1927), Duerden (1902), Gardiner (1903) and others have treated these forms as important agents of disintegration of calcareous rocks and skeletal debris. These algae bore into calcareous material from slightly above the high water mark to some forty meters below sea level (Nadson, 1927, p. 897). However, as Nadson states (1927, p. 1016), "It is particularly in the surface beds of the zone innundated by waves and the tide, that they are active." He lists the following species as most widely present: *Gomontia polyrhiza* and *Ostreobium queketti* of the green algae; *Mastigocoleus* and *Hyella caespitosa* of the blue-greens. Dr. Francis Drouet of the Chicago Natural History Museum, has examined some intertidal material from Florida and states (personal communication, May 2, 1953) that *Entophysalis deusta* and *Plectonema terebrans* are the most abundant forms, with *Mastigocoleus testarum* and *Gomontia* occasionally present.

Practically all of the exposed rock and debris in the intertidal zone is discolored. Broken fragments reveal a greenish rind of boring algae of the order of several millimeters in thickness. Nadson (1927, p. 1017) states that boring algae attack all carbonates including calcite *(Lithothamnions)* and dolomite. Duerden (1902) reported that echinoderms (calcite) are free of algal borings. Examination of thin sections of beachrock from the Dry Tortugas shows that boring algae are

FIGURE 4. Intertidal erosion of Key Largo limestone, Largo Sound.

relatively less abundant in the calcitic *Lithothamnions* than in aragonitic coral and molluscan detritus. Figure 6 show that the intense boring activity occurs on the exposed surface of beachrock. Algal filaments extending into a fragment of mollusk shell similar to the one shown in Figure 6, indicate that algae accomplish the boring and are

not occupying previously formed tubes. Grains a short distance from the surface show borings, but as these borings nowhere penetrate the precipitated aragonite cements, they must have been developed prior to lithification.

The activities of boring algae together with other rock-weakening and destroying organisms, might be expected to produce a regular rock surface in homogeneous rock. One might expect irregular projections to be most attacked because of their increased surface. However, the rapid drying of such projections, as the tide recedes, may make them less habitable to organisms. Also the surficial hardening, whether related to the boring algae, or a phenomenon similar to beachrock cementation, may assist in the preservation of such projections. As was indicated above, aragonitic skeletons, particularly coralline and molluscan, seem most susceptible to boring algae. It is not known whether this relation is due to skeletal texture or mineralogy. Such preferred attack could produce irregularities in a rock containing calcite and aragonite.

Many other attached algae inhabit the intertidal zone, often covering the rock with a felt-like layer. Most of these surface forms probably do not actively bore. However, their attachment by filaments extending into the rock assists in erosion on a small but perhaps important scale.

Bonar (1936) described a boring fungus from the shells of intertidal mollusks in California. The honeycombing action of this organism is often so intense that classification of the shell is difficult. Bacteria may also contribute to intertidal erosion by using calcium carbonate to neutralize acid waste products.

Discussion

Relative Effects of Boring and Burrowing Organisms. It was not possible to make any quantitative estimate of the cumulative effects of boring and burrowing organisms. On most of the shores examined, macro-animals are abundant and boring algae are invariably present. Usually the density of animal borers is greatest below mid-tide but it shows considerable horizontal and vertical variations on a single shore, and the more thoroughly eroded and honeycombed exposed portions are often practically devoid of these forms. This condition indicates the probability of a local progressive development of intertidal erosion. Initially, both boring animals and algae attack the

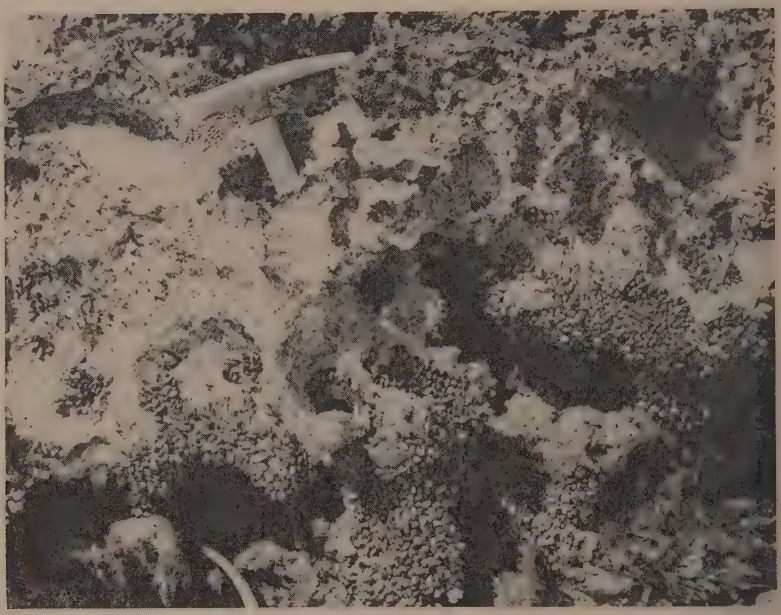

FIGURE 5. A portion of the rock shown in Figure 4, showing the typical honeycombing. The mollusks are *Brachidontes exustus*.

exposed rock but the surficial induration which accompanies erosion produces a spongework of rock which is more resistant than the original limestone. Where wave action is restricted, a greater than usual thickness of this residual rock remains and the attack by animal borers is reduced and probably occurs only well below the exposed surface. However, algae continue to erode the exposed rock.

The differential attack which produces intertidal erosion is a result of the local distribution of borers and the accompanying induration. If original rock texture controlled erosion, beachrock, whose cementation has slight vertical variations, would show a different type of erosion than other limestones.

The general abundance of rock fragments on the inner edge of the lower platform and in depression where erosion is most intense, indicates that the weakening effect of borers, combined with wave action,

is probably as important as the actual removal of calcium carbonate by borers and raspers. The rock fragments are eventually reduced to sand-sized particles by boring and burrowing organisms.

Physico-chemical solution of calcium carbonate caused by unbalanced respiration (Emery, 1946), by acid-charged waters from decaying vegetation, and by rain certainly contributes to intertidal erosion. However, as there are many shores on which these solution processes can be of only minor importance, they are not sufficient to explain intertidal erosion in general.

Submarine and Subaerial Erosion. Examples of erosion generally similar to the intertidal case can be found both above and below sea level. On the Miami Rock Ridge in South Dade County, erosion of the surface limestone, the Miami Oölite, locally produces a pitted and honeycombed rock with irregular projections, resembling intertidal

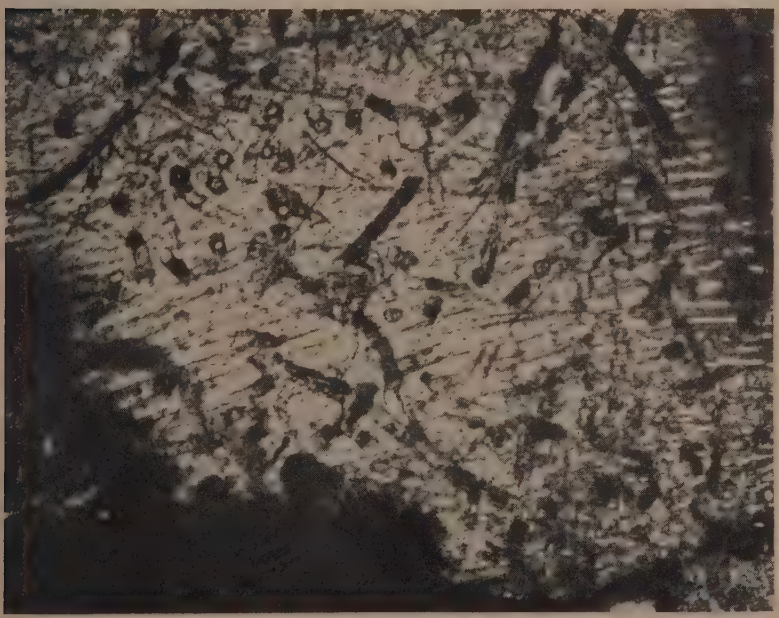

FIGURE 6. Thin-section of the surface of beachrock from Loggerhead Key, Dry Tortugas, in plain light, x 180. Boring algae are abundant in the fragment of mollusk shell.

rock. The surfaces of reefrock from as deep as thirty feet below sea level are also pitted and honeycombed, and if exposed they would be difficult to distinguish from the intertidal surface.

Physico-chemical solution of calcium carbonate by rain water is usually considered responsible for solution of limestones above the water table. However, Krasilinikov (1949) recognized a significant decomposition of bare mountain limestones by the surface microflora, and similar effects are to be expected near sea level in the tropics.

The submarine erosion of reefrock is certainly the result of boring organisms coupled with the preserving effect of the incrusting algae which form a calcareous coating over all but living organisms, difficult for the borers to penetrate.

On the basis of these preliminary observations, it is considered possible that organisms as weakening agents and as direct removers of calcium carbonate play a major role in the surficial erosion of calcareous rocks both above and below sea level. Macro-animals are probably most important below low tide while micro-organisms predominate above that level. Further study of the distribution and effect of epilithic organisms and the several types of physico-chemical solution is required to evaluate the relative roles of these processes.

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The degree of comprehensiveness of the bibliography is to a large extent dependent upon the cooperation of workers in the Marine Sciences of this area. *It is therefore hoped that individuals and organizations will aid by sending copies of all relevant publications to the Editor.* Any omissions brought to the attention of the Editor will be included in subsequent issues.

It has been found convenient to use a modification of the classification used by the Journal du Conseil Bibliography for present purposes.

The Editorial staff wishes to acknowledge the valuable assistance given by a number of investigators in compiling the bibliography.

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Instructions for Preparation of Manuscripts

CONTRIBUTIONS will be considered which deal with research in the marine sciences, directly or indirectly related to the southeastern United States and the Caribbean area. Papers dealing solely with the economic or applied aspects of commercial fisheries will not be accepted.

Manuscripts may be submitted in languages other than English but publication will be in English only. Where possible, arrangements will be made for translation.

All copy should be typewritten and double spaced. Footnotes should be avoided as far as possible. If used they should be numbered continuously throughout the paper and set off in the body of the text.

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